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# The BOTANICAL GAZETTE

FOUNDED BY JOHN M. COULTER

## OCTOBER 1927

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Volume LXXXIV Number 2

# THE BOTANICAL GAZETTE

A JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

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September and October 1927

## A New Old Testament

As advance accounts in the newspapers some time ago intimated J. M. Powis Smith of the University of Chicago, Theophile J. Meek of the University of Toronto, Alex. R. Gordon of the United Theological College and McGill University, and Leroy Waterman of the University of Michigan, have completed their American Translation of the Old Testament. The excitement that the new version has caused in the daily press recalls that brought forth by the appearance of the Goodspeed translation of the New Testament four years ago.

While controversy rages the translators let the matter rest as stated in their Preface to the translation:

"Why should anyone make a new English version of the Old Testament? With the Authorized Version of King James and the British and American revisions, to say nothing of unofficial renderings, have we not enough? This question may quite fairly be asked. The only possible basis for a satisfactory answer must be either in a better knowledge of Hebrew, or in a fuller appreciation of fundamental textual problems, or in a clearer recognition of poetic structures, or in such a change in our own language as would render the language of the older translations more or less unintelligible to the average man of our day. As a matter of fact, our answer must be found in all of these.

"The most urgent demand for a new translation comes from the field of Hebrew scholarship. The control of Hebrew vocabulary and syntax available to the scholar of today is vastly greater than that at the command of the translators of the Authorized Version, or of its revisers.

"Modern studies of textual problems reinforce the need for a new rendering. . . . . The science of textual criticism has made great progress in recent years, and no translation of the Old Testament can afford to ignore its results. Our guiding principle has been that the official Massoretic text must be adhered to as long as it made satisfactory sense. . . . .

"Much of the text that has long passed as prose is now recognized as really poetic both in form and spirit. This adds to the necessity for a new translation. Poetry should not be printed as prose. The present translation brings into clear light many of the hidden beauties of Hebrew poetry. . . . .

"The English of King James's day is not wholly natural or clear to the average man of the present day. . . . . The use of 'vinegar' in the sense of a wine or liquor for drinking has long since ceased to be recognized. . . . . Facts like these make the reading of the Bible a scholarly rather than a religious exercise, and clearly point to the need for a new translation. . . . .

"The content of the Old Testament is, with little exception, on a high literary plane. The language of the translation, therefore, cannot be allowed to fall to the level of the street. In this translation the foregoing principles have been kept clearly in mind. It tries to be American in the sense that the writings of Lincoln, Roosevelt, and Wilson are American . . . . it aims at being easily understood wherever English is spoken. . . . .

"The translators and the University of Chicago Press have sought to give this translation the appearance of a modern book. This purpose has determined the make-up of the page and has led to the addition of headings for paragraphs, and to the *insertion of half-titles before* individual books. It has also kept verse numbers out of the text and relegated them to the margin. . . . ."

In the best tradition of modern English writing this new version interprets the impressive, eloquent Hebrew of centuries ago.

The following passage from "The Song of Songs, Which Is Solomon's" is illustrative of those sections which the translators have cast into poetic form:

THE MAIDEN TO THE YOUTH

Kiss me with kisses from your mouth,
for your love is better than wine;
the fragrance of your ointments is sweet;
Your very self is a precious ointment;
therefore do the maidens love you.
Take me along with you, let us hasten;
bring me, O king, into your chamber,
That we may exult and rejoice in you,
that we may praise your love more than wine;
rightly are you loved.

And here is a part of the story of Ruth in the new translation:

RUTH'S APPEAL TO BOAZ

Then her mother-in-law Naomi said to her,

"Should I not be seeking a home for you, my daughter, where you may be comfortable? Now then, what about our relative Boaz, with whose women you have been? See, he is going to winnow barley at the threshing-floor tonight. Wash and anoint yourself therefore, put on your best clothes, and go down to the threshing-floor; but do not let your presence be known to the man until he has finished eating and drinking. See to it, however, when he lies down, that you note the place where he lies; then go in, uncover his feet, and lie down yourself; he will let you know what to do."

"I will do just as you say," she responded.

So she went down to the threshing-floor, and did just as her mother-in-law had instructed her. When Boaz had eaten and drunk, and felt content, he went to lie down at the end of the grain-heap. Then she came in stealthily, uncovered his feet, and lay down. At midnight the man started up, and turning over, discovered a woman lying at his feet!

"Who are you?" he said.

"I am Ruth, your maidservant," she said. "Take your maidservant in marriage; for you are a near relative."

"May the Lord bless you, my girl!" he said. "This last kindness of yours is lovelier than the first, in that you have not run after the young men, either poor or rich. And now, my girl, have no fear; I will do all that you ask; for all the counselors of my people know that you are a fine woman. . . . ."

*THE OLD TESTAMENT: AN AMERICAN TRANSLATION*. Edited by J. M. Powis Smith. *Cloth $7.50, leather $10.00, postage 25 cents extra.*

## *Silly? Crazy? Damnable Heresy?*

Since the appearance of his *Jesus: A New Biography*, Shirley Jackson Case has been heralded from the Atlantic to the Pacific by newspaper reporters as the arch-heretic of the century. Dr. Case, in attempting to show the modern reader "not the Jesus of the stained-glass window, but the Jesus who lived and walked with men," has, it seems, done something exceedingly sensational. The feeling of the publishers about the matter, however, has been expressed by the Nashville *Presbyterian Advance*, a by no means radical magazine, better than they could do it themselves:

"It appears that Professor Shirley Case, who has published several excellent volumes, has written a book on the life of Jesus. It is not yet published. [It has since appeared.] Some newspaper writer, however, learned something about the book and wrote a sensational story affirming that in the new book Dr. Case declares that Jesus did not affirm his own divinity. Whether this is a fact or not remains to be seen, but on the basis of the assertion of the 'exclusive story' (unfortunately the word 'exclusive' in such cases has come to have about the meaning of 'lying' to discriminating readers) other reporters got busy and interviewed some ministers. These ministers, without having seen the book, promptly proceeded to call it 'crazy' and 'silly' and at least two of them are quoted as calling it 'damnable heresy.' If there is

anything 'crazy' or 'silly' about the whole business, it is to be found in those persons who so violently denounce what they know absolutely nothing about, except on the 'say-so' of some untrained reporter who is probably unable to distinguish between theological dogmas and historical facts."

Hasty and popular as they are, entirely oblivious to the unique methods of scholarship upon which Dr. Case's biography rests, the newspaper accounts have nevertheless shown one significant thing: that the public is intensely interested in new interpretations of Jesus' life and work. The modern reader is eager to look back over the intervening centuries to Jesus as he actually was.

Professor Case has long been known as a scholar who has studied, more fruitfully, perhaps, than any other, the social background of early Christianity. His method has been his most original contribution. It has enabled him to bring the reader of today into direct contact with the environment of beginning Christianity. It enabled him to dispel in his *Historicity of Jesus* the recurring hoaxes that treat Jesus' existence as a myth. And it has now made it possible for him to bring the reader closer than ever before to the real Jesus of history, as he appeared to the men of his own time in Palestine over 1900 years ago.

Within the past few years there have been many unhistorical and sentimental lives of Jesus, but there has not been a biography dealing in so thoroughgoing a fashion with the results of scientific investigation.

*JESUS: A NEW BIOGRAPHY.* By SHIRLEY JACKSON CASE. *$3.00, postpaid $3.15.*

* * *

## *The Ten Princes*

Somewhere beyond the Himalaya Mountains lies Magadha, a land notorious for its unscrupulous delight in sensuous beauty and its ribald worldly wisdom. From this country, at a time when its people were gay, in love with poetry and pleasure, and shamelessly given to lying, fared Rajavahana and nine companion princes to conquer the four quarters of the universe. Dandin told the story of their adventures over a thousand years ago in *The Ten Princes*, his only prose novel. Arthur W. Ryder has retold it in a translation which retains the beauty of the original and adds a modern piquancy.

It seems that Rajavahana disappeared, and the nine companion princes, scattering to find him, met with a series of gay adventures in the course of which each gained a throne and an incredibly beautiful lady. Mr. Ryder's translation is a racy re-telling of Dandin's record, first of Rajavahana's experiences, and, as the other princes rejoin him, of their own exploits, related by them with appropriate flourishes and due exaggeration.

In these adventurers runs a pronounced strain of the picaresque. But rascals as they undoubtedly are, they must nevertheless be accredited with pleasant accomplishments. Handsome as no other mortals, erudite in ethics, astronomy, and metaphysics, they have a gift for the lute, are masters of magic, excel in horsemanship, and possess a scientific skill in thievery, gambling, and the arts of deception in general.

In their travels, they meet many beautiful maidens (versed in the arts of flirtation both major and minor), whom they charm by artifice and natural endowment, and describe in warm detail. And through their stories troop as great a crowd of shady characters, curious villains, and examples of shining virtues, as ever emerged from an oriental fancy: Buddhist nuns, unfaithful wives, sages, rakes, and kings, gay girls and gods, court ladies, merchants, thieves. Each has his appropriate philosophy which the princes remember to the last degree of subtlety, and readily report, whether the subject be the conduct of courtesans or the rules of political science.

Dandin was the master of a beautiful prose

style which has not lost in the translating. One feature of his art is sententious brevity. He looked upon prose as a more exacting medium than poetry itself. Of his life we know little more than that he flourished in India in the seventh Christian century. *THE TEN PRINCES.* Translated by ARTHUR W. RYDER. *$2.00, postpaid $2.10.*

Arthur W. Ryder has also translated from the Sanskrit *The Panchatantra* and *Gold's Gloom.* Achmed Abdulla says of *The Panchatantra:* "Fairytales. But Fairytales for grown-ups. Fairytales suffused with a wisdom that is ironic, slightly bitter, wire-drawn, perfectly civilized. Mr. Ryder's translation is most excellent. It shows not only a thorough knowledge of the subject but understanding, sympathy, style, and a keen sense of humor."

*Gold's Gloom* is bound in exceptionally attractive form, with bright-hued covers, and a specially designed title-page and headbands by Preissig. The quintessence of the wisdom and charm of *The Panchatantra,* it is a representative selection of some of the most captivating stories in the world. *THE PANCHATANTRA. $4.00, postpaid $4.15. GOLD'S GLOOM: TALES FROM THE PANCHATANTRA. $2.00, postpaid $2.10.* Translated from the Sanskrit by ARTHUR W. RYDER.

## *The World and Man*

Critics unite in calling *The Nature of the World and of Man,* by Sixteen Ranking Scientists of the University of Chicago, one of the finest and most engrossing popularizations of current science in existence. A handsome new edition, with bright-hued covers, has just appeared. In accordance with its authors' wish that it should always represent the most recent knowledge of science, revisions have been made throughout the book.

Forest Ray Moulton, the astronomer, says of the volume's theme: "The Nature of the World and of Man is not only a great subject—in fact, the greatest one that human beings may investigate—but it is one rich in romance and filled with stirring adventure. It will satisfy, if anything can, the love of youth for heroic things. The giants of mythological days are far surpassed by the huge machines that are the untiring slaves of modern men. The eye of the fabled Cyclops was not even prophetic of the great telescope on Mount Wilson, the pupil of whose eye, so to speak, is 100 inches in diameter. Not all the magic of antiquity can match the marvels of any chemical laboratory. Physicians cast out demons by means of surgery, by the use of extracts of ductless glands, and by prescribing chemical compounds, and if they have not raised the dead even in a single instance, they have at least within a few decades increased the average span of human life by ten or fifteen years. . . . . In fact, reason and the laws of nature (mark well *reason* and the *laws of nature*) have become a sort of intellectual telescope, as it were, with which modern science looks back across the geological ages. . . . ." *THE NATURE OF THE WORLD AND OF MAN.* By SIXTEEN RANKING SCIENTISTS OF THE UNIVERSITY OF CHICAGO. *$5.00, postpaid $5.15.* (*Textbook Edition $4.00, postpaid $4.15.*)

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Beginning with Melville, Bierce, and Hearn, men who wrote before their time and who belong in spirit to the present

day, Mr. Boynton proceeds to Hergesheimer, Anderson, and Lewis. Believing that it is as necessary for the critic to see and declare what the artist is trying to express as for him to discuss the mode of expression, he conducts the reader to the very center of each artist's own particular world.

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*Some Contemporary Americans*, Mr. Boynton's previous book, still retains its popularity. In it he interprets the drama, the short story, and the poet's art from his background of American life and tradition, and gives his personal reactions to the new modes, forms, and men.

Sandburg, Dreiser, Mencken, Robinson, Frost, Lowell, Wharton, Tarkington, Cabell, Cather, O'Neill, and Bradford appear in this brilliant and engaging series of estimates of contemporary American literature. *SOME CONTEMPORARY AMERICANS*. By Percy Holmes Boynton. *$2.00, postpaid $2.10.*

## *Chinese Painting*

An extraordinarily beautiful volume with fifty-seven plates in collotype is *Chinese Painting* by John C. Ferguson. Chinese art as it really is and as it is valued by the country that fostered it is written into this book with authority and understanding.

Mr. Ferguson's qualifications for judging the art of China by Chinese standards—as it must be done—are many. For thirty-five years he has lived in China in close association with all the connoisseurs and critics of his day, who have been his guides in the examination of extant specimens of writing and painting.

Beginning with the earliest records of China, Mr. Ferguson has written the history of painting in that country to the eighteenth century. The introductory paragraph is characteristic of the spirit of the book:

"More than three hundred years ago Chang Ch'ou wrote in the Preface to his *Ch'ing-ho Shu Hua Fang* that he would like to be transferred into a bookworm, and promised that he would not injure any of the manuscripts or paintings in which he lived, but would be contented with mere existence in their company. Such was the delight with which one of the ablest critics of Chinese writings and paintings reveled in his enormous task of separating the good from the bad, the genuine from the false, among the accumulated ink-remains of previous generations. If Chang Ch'ou could have had his wish gratified by becoming a bookworm, he would not have been of that variety which Emerson placed in contrast with 'Man Thinking,' for he had a keen mind. His wish was the measure of his appreciation of the worthy writings and paintings that came under his observation. These were the products of man's soul and were quite unlike the work of man's hands in bronze or clay or jade. Through these writings and paintings Chang Ch'ou held communion with the spirits of the great artists and calligraphists who preceded him, and in their unseen world there were no limits of time or space." *CHINESE PAINTING*. By John C. Ferguson. *Boxed, $12.50, postpaid $12.75.*

## *Roosevelt*

Turning aside from the hero-worship which has in the past been an almost unavoidable snare to biographers, however desirous of presenting Roosevelt as he actually was, Howard C. Hill has written a book which even at this late date shows Roosevelt in a new light.

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The source material to which Mr. Hill has had access is more extensive than Roosevelt's biographers and historians have hitherto found available. Of this material, the most important part is the Roosevelt papers of the Library of Congress, to which only two or three others besides Mr. Hill have ever been given access. Although perhaps a quarter of his notes were censored by the official in charge, his book still includes the greatest amount of material that has ever been taken from this source.

Roosevelt the man, the creator of the Roosevelt myth, Mr. Hill would place before Roosevelt the statesman. Representative of Mr. Hill's view of Roosevelt in his official capacity is the following: "Rooseveltian imperialism as manifested in the Caribbean was opportunist in character, not planned or predetermined. Like the conscript fathers of ancient Rome, Roosevelt was led from one action to another by the swift current of events which during his administration seemed to change with kaleidoscopic rapidity. . . . . With each problem he dealt in the manner of a practical man of affairs rather than in the fashion of the doctrinaire or the man of predetermined policies."

*The Boston Transcript* comments, "We have Professor Hill to thank for a most interesting glimpse of our ex-President. . . . . He does not hammer away at his conclusions; he presents them gently. . . . . He invites us to strike a compromise, and therefore proves himself a most gracious gentleman, quite unlike any of his kind in the past or present. In his book we find for the student, an essay; for the interested reader, a narrative; for everyone, a striking portrait penned upon a background of living detail."

Harry Hansen in the *New York World* calls Mr. Hill's book "the sober second thought of the historian . . . . a very able study." And the *Herald-Tribune* says, "Professor Hill has turned the X-ray of historical criticism upon Roosevelt's Caribbean policy." *ROOSEVELT AND THE CARIBBEAN.* By HOWARD C. HILL. *$2.50, postpaid $2.60.*

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VOLUME LXXXIV NUMBER 2

THE
# BOTANICAL GAZETTE

*October 1927*

## A WORKING HYPOTHESIS ON THE ORIGIN OF RUSTS, WITH SPECIAL REFERENCE TO THE PHENOMENON OF HETEROECISM

CLAYTON ROBERTS ORTON[1]

Heteroecism was discovered by SCHÖLER in 1818, and was finally established on an adequate experimental basis in 1865, by DE BARY and ORSTED independently. Its origin remains a mystery, however, in spite of the numerous efforts to explain the phenomenon, chiefly on the grounds of the comparative development of the life cycles of the rusts.

FISCHER (**16**) considered the ancestors of our present heteroecious rusts to have been autoecious, but able to live on a wide variety of hosts. In such a plurivorous state, a rust may have been capable of developing its entire cycle upon plants representing the host of the present haploid generation, as well as upon those bearing the diploid. Heteroecism was thought by FISCHER to have originated by a progressive specialization, in which some of the rust offspring acquired an adaptation of their aecial stage to one set of hosts, and the telial stage to a different set of hosts. He believed also that the short-cycle forms originated by reduction and specialization from these same plurivorous parental types.

The earlier views of DIETEL (**10**), which have been adhered to by many students of the rusts, hypothecated the primitive rust as a

[1] Read before the Mycological Section of the Botanical Society of America at the Washington Meeting, December, 1924.

Contribution from the Department of Botany, Pennsylvania State College, no. 59.

short-cycle lepto-form or micro-form, which normally inhabited the aecial host of the present heteroecious species. By extending its vegetative stage to produce aecia and uredinia, it somehow lost its ability to complete this more complex cycle on the one host, and so transferred its sporophytic stage to a different type of host. DIETEL (13) claims to have followed DE BARY'S views on *Chrysomyxa* in regard to the presentation of his early ideas on the origin of heteroecism.

KLEBAHN (25) held that the host-changing species originated from the autoecious fixed types by moving the telial generation to other plants, which he thought was possibly explained by the influence of internal factors, such as mutation. He also considered it possible that the aecial stage was the one transferred to another host in certain cases, and DIETEL (12) also holds this latter opinion, particularly in the case of *Melampsora*. MCALPINE (29) holds essentially the same views as KLEBAHN.

A somewhat different view has been expressed by BARCLAY (4) and GROVE (21), who have proposed that the Aecidiaceae have been derived from *Endophyllum* by amplification and adjustment of the extended sporophyte to a new host.

BLACKMAN (7), on the basis of his discovery of cell fusion in the base of the aecium and nuclear reduction in the basidium, resulting in the establishment of an alternation of generations, presents the probable primitive condition of the rusts from a different angle. He states:

> As the heteroecious forms are confined to those possessing the aecidium, that is, to the more primitive, it seems probable that heteroecism may not be, as generally conceived, a later adaptation, but may actually be the primitive condition in the group. Although we are ignorant of the origin of the group, it is possible to conceive that the sporophyte was first developed in connection with a new terrestrial existence. The autoecious eu-forms would then be the first step in reduction, a purely environmental one; later a morphological reduction of the number of spore-forms would appear to have taken place.

OLIVE (35), in accord with DIETEL'S earlier views, holds the primitive rust to be the short-cycle type, fixed on the present host of the haploid stage. The passing of the extended diploid stage, which he postulates as a later development, to an alternate host, is considered by him to be brought about by the stimulus afforded

by the fusion in the base of the aecium, thus enabling the more vigorous aeciospores to be capable of infecting a new and different host.

More recently DIETEL (13) has reopened the subject, and taken the occasion to revise his views regarding the primitive type. He now concludes that the short-cycle species have arisen generally through reduction, since from their numbers, distribution, and host relationships they can no longer be regarded as primitive. On the other hand, he holds that where a host change was effected, it was brought about generally by the sporophytic stage passing to some other host. In the Melampsoraceae, however, which behave in an opposite manner to the Pucciniaceae, he believes that the original hosts of the oldest forms (like *Uredinopsis*, etc.) were ferns, and that they adopted the Abietineae as new hosts for their aecial stage, when these plants appeared.

ARTHUR (2) believes that the fern rusts show morphological evidences of being most primitive, and that the conditions of heteroecism and pleomorphy were primitive also.

The excuse for reopening the subject lies in the fact that a considerable body of information is now available which either has never been presented in this connection, or has not been given adequate attention. A discussion of the views held by the previous writers will be reserved for the summary.

### Significance of alternation of generations

The alternation of generations persists in the rusts despite the loss of sex organs, indicating certainly that it is an inherent character, and it follows logically that these generations would be separated in the case of heteroecious rusts.

Since the discovery by BLACKMAN of the nuclear migrations and cell fusions at the base of the aecium, and that of SAPPIN-TROUFFY showing that chromosome reduction in the basidium precedes the initiation of the gametophyte, no adequate attempt has been made to point out the significance of these facts in the origin of the rusts and their phylogeny. Compelled as we are to assume that the Uredineae originated from independent plants, one of the most significant features of the group is the fact that a definite alternation of

generations is present throughout, even in the short-cycle forms in which the diploid phase is much reduced. If there is no significance in the alternation of generations conforming to the heteroecious habit, then there would appear to be no reason why the separation in the life cycle of heteroecious rusts should not take place between the uredinial and telial stages, with uredinia borne on the host for pycnia and aecia. This is what might be expected to occur if the contentions of CHRISTMAN (8), MCALPINE (29), and OLIVE (35) are correct, but as yet no rust has been found where such a separation occurs.

The failure of the two nuclei to fuse in the basal cell may possibly be explained on the ground that in the rusts the sex apparatus is lost, and that cell fusion, as DODGE suggests, is secondary like that in the red algae, in which the auxiliary cells take part. That the paired nuclei are not completely antithetic is evidenced by their eventual fusion in the teliospore, and a number of cases are now known where nuclear fusion takes place in the aeciospores. That such an apparent abnormality should occur in a parasitic group of plants and possibly become a permanent condition is not surprising. The fact that certain rusts, such as *Endophyllum uninucleatum* (MOREAU 33), and the uninucleated forms of *Tranzschelia punctata, Ochropsora sorbi* (KURSANOV 26, 27), *Uromyces rudbeckiae* (OLIVE 35), *Endophyllum centrantheri-rubri* (POIRAULT 38, 39), *Kunkelia nitens* (DODGE 15), and other rusts are known to complete their life cycle in the haploid condition only, may be further evidence that the parasitic habit may lead to extreme results even in morphological degeneration.

### Conservation or fixity of organs

It appears logical to expect the most persistent organ in a rust to be homologous with the most characteristic organ of its independent ancestor. Such a relation appears between the teliospore and the tetrasporangium of certain red algae. The doctrine of the conservation of organs holds an important place in phylogeny in the theories of students of the higher plants. Comparative studies of early geologic forms and of related existing ones have shown that certain organs are more likely to persist unchanged than others. Application of this doctrine to the fungi has been restricted for several reasons.

Unfortunately, we are not aware at this time of the presence of any considerable number of fossil rusts to guide us on these points. The few uncertain cases cited by MESCHENELLI (32), however, are aecidioid (Aecidites) and telioid (Puccinites) types, indicating that aecia and telia are the more fixed, and probably the most primitive spore stages of our present rusts.

The teliospore with its basidium appears to represent the most conservative persistent structure of the rusts. I have come to this conclusion after carefully considering the matter from the standpoint of the spore structure most universally present in the group. Strictly speaking, the 4-celled basidium is the most outstanding stage in the development of the rusts, and we can logically consider this as their most conservative structure. It would be logical as well to expect the teliospore as the most conservative organ, since it is a tetraspore mother cell. Reasoning from this standpoint, we can see at once the relationship between the teliospore and the tetrasporangium, since both produce four spores as the result of maturation divisions.

**Effect of acquisition of parasitic habit**

The acquisition of a parasitic mode of life on the part of a plant, formerly independent, produces certain very definite changes. The most prominent is the loss of chlorophyll, and this feature is well represented in numerous algal forms like *Harveyella*, which are parasitic on other algae and show various gradations in loss of chromatophores and chlorophyll formation, apparently in proportion to the degree of dependence attained. SETCHELL and others have noted a number of these parasitic red algae. Other definite changes are embodied in the development of the thallus. This is invariably reduced in size and often in structural differentiation. Such changes certainly point to degenerative processes which may be expected to affect the reproductive parts as well. While the evidence as to how parasitism has with certainty modified reproductive structures in the rusts is not substantiated, unless we admit *Kunkelia nitens* to this category, we can scarcely avoid arriving at the logical conclusion that reductions rather than amplifications are to be expected in any group of obligate parasites. It is difficult to conceive how such a

mode of life, which plainly results in degeneration of vegetative parts, could bring about the opposite effects on reproductive parts, especially such changes as would be involved in the development of a long-cycle from a short-cycle form.

### Length of cycle as indicating trend of phylogeny

The evidence gleaned from a study of the relative numerical importance of the long and short cycle in the rusts, their geographical distribution, their correlations, and their climatic adaptations, indicates clearly that the phylogenetic trend is toward the short-cycle form, in both heteroecious and autoecious species. We conclude, therefore, that long-cycle rusts are the more primitive.

The bearing which the length of cycle of specific rusts holds to the phylogeny of the group has been given considerable attention by FISCHER, DIETEL, MAGNUS, KLEBAHN, and others. Without entering into a discussion of the several views held, it may be stated that the short-cycle rusts have generally been accepted as the more primitive, and have in various ways given rise to the long-cycle forms by amplification of the sporophyte. BLACKMAN (**7**), KURSANOV (**27**), and those agreeing with ARTHUR, have taken the stand from the evidence at hand, that the trend of evolution in this group has been in the opposite direction; that is, that the long-cycle forms are the more primitive, and that the short cycles have originated later through the reduction of the sporophyte. DIETEL, who earlier held the former view, has more recently (**13**) reviewed the whole matter, and come to the conclusion that the latter method is the more likely one. The conclusions of KURSANOV from his independent researches add much weight to this conclusion. The data bearing on this point have been gathered from several sources, and approach the problem from four angles.

1. RELATIVE NUMERICAL IMPORTANCE OF SHORT-CYCLE FORMS.—There are recognized in the North American flora approximately 1200 species of rusts. Of these about 200 are short-cycle lepto-forms or micro-forms. If it is to be considered that the short-cycle rusts are the more primitive, then we are forced to acknowledge that a large majority of our rusts have already undergone a pronounced change by lengthening the sporophytic stage, and if this is the case

we should also expect to find evidences of this lengthening process among our representative species. No such cases are known at present; on the contrary, we feel confident that the opposite condition is now taking place, as is evidenced through the studies of KUNKEL and DODGE upon the two forms of the orange rust of brambles (*Gymnoconia interstitialis* and *Kunkelia nitens*). In this case there can be no doubt that the short-cycle *Kunkelia* has been derived by reduction from the long-cycle *Gymnoconia*. Furthermore, the short-cycle form is apparently undergoing still further changes, as indicated by the recent studies of DODGE (**15**) pointing out a distinct form which he has discovered. There are other rusts which point strongly toward a similar process of reduction, but further proof should be presented. It then appears that the most logical theory, which is upheld by at least one known case, is that the short-cycle rusts are being evolved from the long-cycle forms, which fits best with the data on the relative numerical importance of the two cycles. In this connection it is well to point out, as KERN (**24**) has done, that in the Campanulales, which are acceded to be our most recently evolved flowering plants, the proportion of long-cycle to short-cycle species of *Puccinia* is one to two. This would indicate that the short-cycle forms are in the ascendancy in this order of host plants.

It may be well to point out also, that of approximately 200 short-cycle species known in America, 149 belong to *Micropuccinia*, as delimited by ARTHUR. It must be significant that such a large proportion is to be found in a genus which most uredinologists regard as the most recent in phylogeny, as exemplified by the type of teliospore and structure of its sorus.

2. GEOGRAPHICAL DISTRIBUTION OF SHORT AND LONG-CYCLE SPECIES.—DIETEL (**13**) has presented the most complete data on the geographical distribution of the short and long-cycle rusts, and has shown that almost invariably the short-cycle forms, which are correlated with long-cycle species, are more restricted in their distribution. So far as he knows, only one short-cycle species, *Uromyces phyteumatum*, occupies a wider geographical distribution than its corresponding long-cycle form, *Uromyces caricis-sempervirentis*. Of twenty-three short-cycle forms cited by ARTHUR and JACKSON (**1**) as definitely correlated with eu-heteroecious species, fourteen

have a very restricted distribution; six approach their corresponding heteroecious species in distribution; two are practically coextensive; and one, *Puccinia holboellii*, has a wider distribution than its correlated *P. monoica*. These data agree in the main with those of DIETEL. It might be argued that the long-cycle forms are better adapted to extend their distribution through the possession of the repeating urediniospores, but that such a conclusion is unwarranted is brought out in the next point.

3. CORRELATIONS BETWEEN SHORT AND LONG-CYCLE RUSTS.—When DIETEL (**9**), FISCHER (**16**), and TRANZSCHEL (**41**) established the connections between short and long-cycle rusts, the former occurring on the aecial hosts of the latter, they disclosed a condition of the greatest import in the phylogeny of the group. A considerable list of such species has been compiled by DIETEL (**13**) and ARTHUR and JACKSON (**1**), indicating beyond doubt that a number of the known short-cycle forms are related to the corresponding long-cycle heteroecious species. As DIETEL points out, if the long-cycle forms were derived from the short-cycle ones, it would be expected that the latter would have a wider distribution than the former, because of their host relations. It seems hardly possible that a parasite dependent upon two unrelated hosts should have a wider distribution than one which can maintain its existence upon one host. Yet such is the rule, and leads us to the conclusion that the original form was the long-cycle heteroecious one, and that the reduced form has appeared only in certain restricted localities less favorable for the continued development of several spore stages.

4. CLIMATIC RELATIONSHIPS BETWEEN LONG AND SHORT-CYCLE RUSTS.—FISCHER (**17**) has presented some interesting data on the relative distribution of long-cycle and reduced species in Switzerland. Of the micro-forms, 53.7 per cent were found above the tree limit; of the lepto-forms, 27.3 per cent occurred above this limit; whereas of the eu-autoecious forms only 14.5 per cent occurred above the tree line, and of the eu-heteroecious forms only 17.9 per cent. MAGNUS (**30**) also pointed out the evident fact that the proportion of rusts with short cycles increases with the altitude. No comparable data are available in North America, but table I compares some short and long-cycle rusts belonging to *Puccinia*,

and indicates that there is a greater proportion of the long than of the short-cycle species represented in the tropics, and that a larger percentage of short-cycle species is represented in arctic regions. This indicates that the short-cycle species are more northern in distribution than the long-cycle ones, and possibly aligns the data with those of FISCHER in Switzerland on altitude.

TABLE I

DISTRIBUTION OF DICAEOMA AND MICROPUCCINIA

| | TOTAL SPECIES | PERCENTAGE TROPICAL | PERCENTAGE TEMPERATE | PERCENTAGE ARCTIC |
|---|---|---|---|---|
| Long-cycle O, I, II, III..... | 269 | 52.8* | 60.0 | 2.9 |
| Short-cycle III, or O, III..... | 149 | 34.8 | 71.8 | 10.7 |

* The fact that the total percentage in the three groups amounts to over 100 is occasioned by the overlapping of numerous species; for instance, a considerable number of species occur both in temperate and tropical America, and such were counted in both columns.

Another point that should be borne in mind is that the possession by long-cycle rusts of urediniospores as well as aeciospores, both of which are rather resistant to desiccation, and in addition are wind-borne for long distances, presumably enables them to be disseminated over wider areas. This feature, however, is limited by the extent of specific host specialization.

## Morphological basis

The researches of KURSANOV (**27**) show that the structure of the aecidium, uredinium, and telium are essentially similar, in fact he terms them homologous; and that of these three sori, the first comes nearest to the fundamental type. The hypothesis is thus presented that because of the morphological similarity of these three structures, it is probable that the latter two must have been evolved from the most primitive, and have carried with them the morphological continuity of the aecial primordium.

The important point to be considered here, and one previously almost wholly overlooked or avoided, is whether this evolution took place before the time when the rusts became obligative parasites or after. No convincing arguments have been presented up to this

time showing that any short-cycle rust has evolved into a long-cycle form. OLIVE, CHRISTMAN, LINDFORS, GROVE, and others, who have taken the position that evolution from the short-cycle to the long-cycle types has thus arisen, have failed to take into account two important facts: (1) that progressive evolution is extremely rare among parasitic forms, and (2) that most of the types represented in their studies may be shown to have correlated long-cycle forms, which throws much skepticism on the value of their arguments. KURSANOV faces the situation squarely and comes to the conclusion (without entering into the parasitic argument) that the trend has been from the long to the short cycle by retrogressive processes. LINDFORS (28), while admitting this for certain species (*Uromyces acetosae*, etc.), concludes that the primitive type must have been short-cycle, and cites *Chrysomyxa abietis* as best representing the ancestral rust.

From the facts at hand there does not appear to be any evidence that progressive evolution has taken place in the ontogeny of any species of rust subsequent to our knowledge of this group. We are forced to agree with KURSANOV, therefore, that in the phylogeny of the rusts as such, all the convincing evidence points toward retrogressive changes, either by the omission of intermediate stages (aecia, uredinia, or both), or by nuclear fusion in the aeciospores, thus cutting off the vegetative sporophyte with its accompanying sori, to form the short-cycle types. The exact position of the first binucleate cells in these short-cycle forms is unimportant. The important feature here is that the telia hold the relative position in the cycle which was held by the aecia in long-cycle forms.

The types represented by *Endophyllum* and *Kunkelia*, most of which have known long-cycle correlatives, should not be disconcerting, since it is apparent that two sorts of abbreviation have taken place: (1) the types in which the telial stage has been drawn back to the position of the uredinial or aecial stage by the omission of either one or both of the intermediate structures; and (2) the types represented by *Endophyllum* and others, in which the soric cycle has been cut off at the end of the aecial stage and nuclear fusion takes place in the aeciospores, resulting in the formation of a basidium at the time of their germination. The fact that in certain forms

of *Endophyllum*, in *Kunkelia*, and in *Peridermium*, some of these spores do not produce basidia, but on the contrary produce germ tubes which may even reinfect the alternate host or the same host, as the case may be, does not furnish any evidence that the short-cycle forms are primitive and are thereby becoming long-cycle, but indicates that they are still more or less unstable and have not completely adopted the shortened cycle.

To return to the hypothesis, we find no evidence that short-cycle rusts are becoming long-cycle, but that some other explanation of the continuity of the aecial primordium must be substituted. We know that the rusts, like all other parasites, must have evolved from independent or saprophytic forms; and it seems most logical, therefore, to suppose that such morphological structures and homologies as exist between the various soral structures are merely reflections of their pre-parasitic condition, and more or less modified, of course, by their later environment.

## Homologies with independent plants

Since it appears most logical to assume that the rusts are derived from an independent group of algal ancestors, we must study the comparative morphology of the rusts and the orders of algae. From the standpoint of the evident homologies existing between the several reproductive structures in the rusts and the red algae, coupled with dimorphism in the latter, we conclude that we should look to the red algae as the most logical group from which to derive the rusts.

The relationship which one group of plants holds with another group is based upon the homologues existing in the two groups. When both of such groups are independent plants the problem is difficult enough, but when any attempt is made to homologize the structural features of a dependent with a separate independent group, the problem becomes much more complex. The factors which parasitism injects into the problem cannot be stated in any accurate terms, and can only be approximated by a comparative study of the ontogeny of many individuals within both groups.

Without going further into the details of the evidence as regards the evolutionary tendencies among the rusts, I wish to point out that

all the evidence available at the present time appears to point to the conclusion that within the Uredinales the trend is toward increased physiological specialization, accompanied by morphological reduction through degeneration from the complex to the simple types; that is, from long cycle to short cycle by a shortening of the sporophyte. While this may seem anomalous to students of independent plants, I can come to no other logical explanation of the origin of our common short-cycle rusts. A similar reduction from complex to more simple morphological types is progressing in certain Ascomycetes, as indicated by the studies of FRASER (**20**) and others, pointing to the loss of oogonia and the suggestion of apogamous development. While there may be other reasons for this trend toward simplicity, the effect of parasitism on the parasite through physiological degeneration is apparently the chief contributing factor, and one which has been disregarded largely by those who have sought to build up a theory of phylogeny in this group of fungi.

Assuming that the primitive rusts were long-cycle, we are forced to search for homologies among those independent plant groups where an alternation of generations exists, comparable to that in rusts, and where pleomorphic spore forms are produced. Several writers, notably BLACKMAN (**7**) and YAMANOUCHI (**42**), have already pointed out the similarities between the rusts and the red algae, but none have analyzed this relationship as clearly as DODGE (**15**), who conceives the fusing cells of the aecidial primordia as merely intercalary. He states:

> The fusions are of exactly the same nature as those occurring between the accessory sterile and auxiliary cells in the red algae. . . . . There is no structure in the rusts which takes the place of or is the homologue of an egg apparatus. . . . . It is the lack of the element of femaleness represented by the egg which distinguishes a rust most fundamentally from its ancestral alga.

Furthermore, insufficient attention has been given to the significance of the teliospore together with its germination to produce the four basidiospores. Inasmuch as the teliospore with its basidium appears to be one of the most conservative (fixed) organs of the rusts, its importance in any scheme of phylogeny should be given adequate consideration. The outstanding features of the teliospore are that it terminates the sporophytic generation; it produces the basidium within which reduction divisions take place, with the for-

mation of four cells which generally produce four basidiospores initiating the gametophyte; and it is typically a resting spore with thickened walls. How do these features compare with the condition found among the red algae? In the Florideae the termination of the sporophyte takes place with the formation of the tetraspore mother cell. Within this cell reduction takes place, followed by the formation of four tetraspores which initiate the gametophyte. The tetraspore mother cell is usually thick walled, and frequently functions as a resting sporangium. It appears that the following homologies are indicated: the 1-celled teliospore is homologous with the tetraspore mother cell; the 4-celled basidium is homologous with the four tetraspores.

Whether there is much significance to be attached to the various types of teliospores among the rusts, in so far as they may indicate ancestral traits, is not clear. Certainly if we would search for a teliospore in the rusts which has the most striking likeness to tetrasporangia, we should cite the teliospores of *Uredinopsis*, *Hyalopsora*, *Milesia*, and other fern rusts. Among these may be found frequent examples of a tetrad arrangement of the teliospore cells, recognizing, of course, that the teliospores here are homologous with an aggregate of tetrasporangia. Perhaps of further significance is the lingering tendency observed among certain fern rusts to form their teliospores singly on the mycelium rather than in aggregates to produce sori.

The phenomenon of basidial formation within the teliospore so characteristic of the Coleosporiaceae should not be overlooked. The analogy here indicated with the tetrasporangium is most striking, and may indicate the most primitive conditions existing among the rust fungi. We should not overlook, of course, the possibility that the Uredinales are polyphyetic, and that the three families generally recognized are of separate origin. In the face of the argument of DIETEL (14) and others, that the Coleosporiaceae is a primitive group, it seems possible that this family may have been derived from a different line of ancestors, and is of more recent origin than the Uredinaceae. This might account also for the wider separation of the alternate hosts of the Coleosporiaceae, as well as the retaining of the characteristic formation of internal basidia.

As regards possible homologies with other spore structures of the

red algae, we must, of course, note the apparent relationship of the aecidium with the cystocarp. Without entering into the controversy over the morphological relationship between the red algae and the Ascomycetes, it appears pertinent to indicate, from KURSANOV's (**27**) studies, that the aecidium is to be considered the primary fructification of the rusts, and that striking similarities occur between this organ and the cystocarp. The fact that in both of these organs the sporophyte is initiated from the gametophyte is fundamental. While it is true that in most rusts nuclear fusion is delayed, it appears probable that the present hyphal conjugation is to be regarded as a process which has arisen through degeneration as a substitute for some more elaborate process, such as exists in the red algae. The reasons for such degeneration may be attributed to the acquisition of the parasitic habit without overworking the idea of degeneration through parasitism.

While we cannot with certainty homologize the fertilized carpogone with the fusion cells of the aecidium, it is apparent that the carpospores are homologous with the aeciospores. Other relationships are suggested, but must await more detailed studies.

The question also arises regarding the origin of the uredinia, with their very characteristic echinulate urediniospores. One might be inclined to assume a relationship between urediniospores and the monospores of the red algae, but so little is known regarding the latter that it is hardly possible at this time to make further suggestion.

Of special significance is the discovery of HOWE (**22, 23**) that dimorphism exists among the red algae, and that the carpospores of *Galaxaura* undoubtedly produce on germination a structurally distinct sporophytic plant, which in turn bears tetraspores which eventually complete the dimorphism by producing the gametophytic plant. This condition is not unique for the red algae, since SAUVAGEAU (**40**) has established a similar condition in the Laminariaceae of the brown algae, and it seems probable that eventually we shall find this condition rather common, at least among the red algae. It is not improbable, as has been suggested by others, that a number of the red algae known only in the carposporic or tetrasporic stages represent one stage only of dimorphic species.

It would appear that HOWE's discovery very probably bears directly on the relationships which are apparent between the red algae and the rusts. If we consider the ancestors of the rusts to have been independent algal plants, we could not hope to point out a closer relationship than is now apparent between the dimorphic Florideae and the heteroecious rusts. The life cycles are as nearly identical as can be expected to exist between two groups, one independent and the other dependent.

The view of C. E. BESSEY (5), E. A. BESSEY (6), and others, that the rusts originated from the Ascomycetes, seems highly improbable in the face of all the evidence presented. There would seem to be no convincing analogy between the two most fixed organs of these groups, that is, the teliospore and the ascus; neither is there any very close relationship between the aecium and the ascus. If the rusts had been derived from the Ascomycetes, we should certainly expect to find more striking structural similarities between the two groups, and especially between the parasitic representatives of the Ascomycetes and the rusts. The absence of any real significant structures common to Ascomycetes and the rusts leads to the conclusion that the former had their origin from a different order of plants, or at least from a different group of the red algae than that giving rise to the rusts.

FITZPATRICK (18, 19), in his studies on *Eocronartium muscicola*, brought forward the hypothesis, earlier suggested by ATKINSON (3), that the Uredinales may have arisen from forms similar to those now included in the Auriculariaceae, on the basis of the apparent parasitism of certain members of this group, but more especially on the evident homology between the cell of the teliospores in the rusts and the cell giving rise to the basidium in the Auriculariaceae, and the general similarity between the cross walled basidia of the two groups. While these similarities must be conceded, there appears to be little else in common between the rusts and the Auriculariaceae. In so far as the investigations on this last group have progressed, there is no evidence of a fixed alternation of generations, and particularly of any such definite and outstanding feature as the haploid mycelium in the rusts. It would appear more logical to grant a similar origin to the two groups, as indeed practically all mycologists

have done for the Basidiomycetes as a whole, but without acknowledging for the present the evolution of the one from the other.

### Significance of host relationship of heteroecious rusts

Since what appear to be the most primitive rusts inhabit ferns and a number of the Pinaceae (*Abies*), it seems probable that these plants represent the original hosts of the Uredinales, and that heteroecism was established on them. The phenomenon of heteroecism is found throughout the Uredinales and nowhere else among the fungi, unless we admit certain species of Ascomycetes (*Sclerotinia heteroica*). That this remarkable condition should be so strictly limited to a single order of fungous parasites indicates that it is of significance as regards the origin of the group. If this phenomenon was correlated with any definite host relationship, its origin might be explained on other grounds, but all students of the rusts have commented on the lack of any apparent relationship between the alternate hosts of the heteroecious rusts. If heteroecism arose by the sudden jumping of one stage of a rust to some other unrelated host, as some workers believe, or if it arose through the gradual restriction of hosts from a plurivorous condition, as others are inclined to think, we are led at once to question why the rusts have so exclusively developed this habit.

On the grounds of pleomorphy, parasitism, and purivory, there is no apparent reason why heteroecism fails to appear more generally in the Ascomycetes, and also in the Oomycetes and the higher Basidiomycetes. Its failure to appear in these other groups may indicate that they had a different origin from that of the rusts. Surely if the Ascomycetes and the rusts both originated from the Florideae, we should expect to find in the former some indication of this phenomenon of heteroecism so outstanding in the latter. Even though the impossibility of separating the ascocarp from the gametophyte precludes the establishment of heteroecism in the Ascomycetes on the basis of the alternation of generations, still heteroecism is not necessarily dependent upon such a separation. It would appear, therefore, that some fundamental difference existed between the ancestors of the rusts and the Ascomycetes which has been the chief factor in determining heteroecism in the former. Such a differ-

ence may possibly have been dimorphism of the sort previously discussed.

While we admit that little, if any, relationship exists between the alternate hosts of heteroecious rusts, we find in certain genera, especially of the Uredinaceae, a closer relationship between such hosts than is shown in the Coleosporiaceae and Aecidiaceae. It will be worth while to point out here that among those genera of rusts which are parasitic on ferns (*Uredinopsis*, *Hyalopsora*, and *Milesia*), the alternate host in each case is a species of *Abies* belonging to the Pinaceae. Nowhere else do we find so close a relationship between the alternate hosts of rusts. As already pointed out, there are excellent indications that these particular rusts are primitive, as indicated by the structure of the teliospore and in numerous instances its poorly defined sorus. If such a supposition should prove to be the case, we might hypothecate that the rusts originated as such in a period typical of ferns and conifers, and that these two groups represent the primitive hosts of the Uredinaceae. ARTHUR (2) goes further and suggests that the fern rusts represented by *Desmella* are primitive forms of Pucciniaceae. This particular genus inhabits ferns belonging to the Polypodiaceae and Schizacaceae, which are presumably of more recent origin than the Osmundaceae, which harbors *Uredinopsis* and related rusts. It is not improbable, therefore, that both heteroecism and autoecism developed in such a period, and that the segregation of the rusts took place during such an early time.

### Correlations between various species of rust

Correlated species of rusts are most prevalent in *Puccinia* and *Uromyces*, which have been considered the more recently evolved types. Since many of these correlations involve short-cycle forms, additional evidence is adduced that primitive rusts are long-cycle.

No attempt will be made here to present a list of correlated species, but rather, by the following grouping, to show what sort of correlations exist, and point out a few significant points which seem to bear on the origin of certain species. All of the following examples are taken from the two largest genera of rusts, *Uromyces* and *Puccinia*. Parallel correlations are to be found throughout the

order, but not so frequently as between species belonging in these two genera.

From a study of the following cases it is evident that at least three different types of correlation are present, as follows: (1) Correlations between autoecious and heteroecious species of eu-*Puccinia* and eu-*Uromyces* in which the only difference lies in the number of cells in the teliospore. From the fact that in general the 1-celled form is less widely distributed, and as the writer has remarked (**36**), appears less vigorous than its correlated 2-celled form, it appears most logical to suppose that the 1-celled race was derived from its corresponding *Puccinia*. If this is true, here again we have evidence of degeneration taking the form of dropping one cell from the teliospore. The presence of mesospores in the telia of many species of *Puccinia* further indicates this trend. (2) Correlations between heteroecious eu-*Puccinia* and micro or lepto-*Puccinia*, in which the latter develops telia on the gametophytic host of the former. These correlations are very common, and have been known since TRANZSCHEL noted the classical case of *Tranzschelia punctata* and *Polythetic fusca*, and DIETEL (**9**) mentioned the case of *Puccinia mesneriana* and *P. coronata*. (3) Triple correlations between autoecious species of eu, opsis, and lepto or micro-*Puccinia* which have been discussed briefly by the writer (**37**), who believes the opsis-forms to be intermediates between short and long-cycle autoecious rusts. This is indicated by the rather frequent presence of urediniospores in the telia of the opsis forms, and aeciospores in the telia of the micro and lepto-forms, indicating that uredinia disappear first and aecia later.

All of these correlations seem to be explained most clearly on the basis of the simpler forms having been derived from the more complex, by reduction or the dropping out of some structure or stage. That this reduction is not confined to the sporophyte is evidenced by the fact that a large proportion of the reduced forms have also dropped the pycnial stage and are now represented by telia only.

### Effects of evolutionary progress of host upon host relations

It seems quite possible that the phylogeny of the plants which now serve as hosts of heteroecious rusts had an important bearing upon their present wide separation in the system of classification.

It seems unlikely, as DIETEL (11) points out, that a group of obligate parasites, like the rusts, could have passed through the many evident changes which have taken place and are still continuing, without being affected by the evolutionary processes of their host. While the antiquity of the rusts (relative to the higher plants which serve as hosts) is unknown, it seems probable that they date back at least to a period where phylogenetic lines in the higher plants were being evolved.

If we should ever be so fortunate as to establish the origin of parasitism in the rusts before or at the time of the supposed origin of the phylogenetic lines derived from the Ranunculaceae, we should have to postulate an association which has since that time passed through many vicissitudes, during which some less fortunate groups have been left behind, and the more fortunate ones evolved into our higher types of vegetation. Is it not probable that during this progress in the evolution of the higher plants the segregation of the rusts has gone on in a similar manner? For instance, why do we find a unique genus like *Uromycladium* confined solely to one genus of host plants as *Acacia*? In the same way, why is *Ravenelia* confined to Mimosaceae and close relatives? While the writer does not propose to make a thesis of this point, it certainly seems probable that we have had a wide segregation of the rusts coincident with their parasitic development. May it not be possible that the wide separation of the gametophytic and sporophytic hosts, as in the case of many heteroecious rusts, has come about through the more rapid evolution of one host than the other?

## Significance of antithesis between gametophyte and sporophyte in light of physiological responses produced by each on their host plants

The antithetic responses produced by the alternate phases of rusts indicate their origin from ancestors in which the gametophyte and sporophyte were vegetatively independent of each other.

In studying the pathological responses produced by rusts an interesting fact has appeared, that is, that with very few exceptions the most outstanding deformities are produced in the host by the gametophytic mycelium. This is evident in both heteroecious and

autoecious species. Two or three typical examples will serve to illustrate the point. *Uromyces proeminens*, an autoecious long-cycle rust, produces in its gametophytic stage a conspicuous change upon its host *Euphorbia*. In this stage the rust is systemic and causes etiolation and an upright habit of growth of its host, accompanied by leaf dwarfing. In the sporophytic stage the rust is not systemic and does not cause any pronounced symptoms. A very similar effect is produced by a group of heteroecious rusts well represented by *Uromyces pisi*, having their gametophytic mycelium in *Euphorbia* and the sporophytic in Fabaceae. Marked changes in form of host occur in *Euphorbia*, but nothing noteworthy in symptomatic effects is produced by the sporophyte. A considerable number of short-cycle rusts also show this particular type of symptom. A typical example is *Puccinia holboellii*, a short-cycle rust on *Arabis*, which is systemic, producing dwarfing and sometimes a witches' broom effect. Its long-cycle correlated species *Puccinia monoica* bears its gametophytic stage on *Arabis* and its sporophytic on two grasses, *Koeleria* and *Trisetum*. In the former phase the same symptoms are produced on *Arabis* as are produced by *Puccinia holboellii*. The species of *Cronartium* present an analogous condition. The gametophytic stage on *Pinus* produces galls and swellings of various sorts, while the sporophyte produces no such effects. These phenomena indicate that the effects produced by the gametophyte of a short-cycle rust are comparable with the effects produced by the same mycelial generation of a long-cycle rust, irrespective of the associate spore stages. There is, then, not only a fundamental morphological distinction between the gametophyte and the sporophyte, but the distinction is linked with fundamental physiological differences in effects produced upon their hosts.

These significant antithetic effects produced independently by the two stages of rusts can hardly be due to host relations, or to the types of tissue invaded by the respective phases. It must be more fundamental, and it would appear logical to trace it back to a separate origin for each stage, such as would be expected if these rusts originated from dimorphic ancestors similar to the condition now known to occur in the red algae.

## Summary

1. Little attention has been given to the significance of the haploid and diploid generations in the rusts, in the light of their similarity to the alternate generations in the algae on the one hand, and their correspondence with the heteroecious habit of the rusts on the other hand. BLACKMAN calls particular attention to the close analogy with the red algae in discussing the relationships of the Uredineae, and YAMANOUCHI draws a similar analogy in his discussion of the relationship of one of the red algae, *Polysiphonia*, with the rusts. Other writers also have mentioned this analogy, but have not made a point of the separation of the generations corresponding with the heteroecious habit. It is certainly significant that the antithetic generations of mycelium are invariably separated on unrelated hosts in all heteroecious Uredinales.

2. While the structural similarities existing between the rusts and the red algae are striking, it appears that they are supported by certain homologies between the two groups. The teliospore is homologous with the tetrasporangium, the basidium with the four tetraspores, and therefore the gametophytic thalli of the two groups are homologous. Since the pycnia of rusts and the male conceptacles of red algae are borne on the gametophyte and show striking similarities in structure, it seems possible that they are homologous, in which case the pycniospores are homologues of the spermatids. So far as the evidence has been presented, it appears that the aeciospores of rusts may be homologous with the carpospores, and since both produce the vegetative sporophytes, the latter are homologues. Of further significance is the close analogy between the functions of the corresponding homologous organs. It would be difficult to find a closer apparent relationship between two groups of plants, one independent and the other dependent.

3. Our knowledge of fossil rusts is very meager, but of the few species described, only aecial and telial stages are known. This certainly indicates that these are the most conservative organs of the rusts, and this is borne out by our knowledge of present day rusts. We may conclude, therefore, that primitive rusts possessed both the aecial and telial fructifications.

4. The trend of phylogeny in the rusts is indicated by a comparative study of their life cycles. The relative numerical importance of long and short-cycle rusts is greatly in favor of considering the short-cycle forms as arising by reduction from the long-cycle species. The short-cycle rusts constitute less than 20 per cent of the total species; they have a much more restricted geographical distribution as well as climatic adaptation; and a large number of them are already known to be definitely correlated with long-cycle species, which certainly appear to possess the more primitive characters. In addition to these points, the proportion of long and short-cycle species of *Puccinia* inhabiting the Campanulales is about one to two, indicating, as KERN (24) has pointed out, the probability that the short-cycle forms are the more recent. The fact that reduction has taken place is clearly shown in the case of *Kunkelia nitens* being derived from *Gymnoconia interstitialis*.

5. The acquisition of the parasitic habit invariably results in degeneration, as indicated by the loss of independence through the disappearance of chlorophyll and chromatophores, a reduction in the size of the thallus, and probably a reduction in its structural differentiation. The evidence is all in favor of reduction in morphological structures through the loss of uredinia, aecia, and pycnia, as well as reduction in the number of cells in the teliospore. An increasing host specialization indicates still greater dependence in food relations which can only be interpreted as tending toward further degeneration and reduction to the simplest types which produce telia only.

6. The importance of the host relations of heteroecious rusts is of special significance, because this phenomenon is characteristic only of this order of parasitic fungi. If heteroecism arose by a sudden jump from one host to another, it is curious that it has not appeared in such groups as the Oomycetes, Ascomycetes, and the smuts; and further, we should expect the jump to have been made in some cases to closely related hosts. Since the evidence is all negative from these standpoints, we must conclude that the phenomenon of heteroecism has a different origin. If the heteroecious habit was derived from the autoecious by a gradual restriction of the two generations to separate hosts, we should again expect to find heteroecious rusts passing

their alternate stages on closely related plants, at least in some cases. The evidence is also negative regarding this point, and we are forced to conclude that heteroecism is an ancient feature of the group.

7. The existing correlations between heteroecious and autoecious species, coupled with correlations between long and short-cycle species, all point to the heteroecious and long-cycle autoecious species as being the most primitive. We can agree with FISCHER that the primitive rusts were probably plurivorous, but we cannot subscribe to his ideas as to the manner in which heteroecism arose. FISCHER's ideas regarding the origin of the short-cycle forms seem sound in general, and DIETEL's recent views regarding the origin of the short-cycle forms from the heteroecious species appear logical in the light of the evidence as he has presented it, and as we conceive the phenomenon. There would seem to be no reason, however, why he should retain the idea of host changing in special cases by sudden jumps, as, for instance, in the case of the fern rusts, which according to him appear to have transferred their gametophytic generation to *Abies*, or why he should believe that a similar sort of change took place in *Melampsora*. In the same way we must reject the proposals of KLEBAHN, OLIVE, and others who have postulated the jumping of the sporophytic stages to a separate set of hosts.

The theories of BARCLAY and GROVE regarding *Endophyllum* are more logically explained on the ground that this genus represents a reduced type similar to *Kunkelia nitens*, which has been derived simply by the fusion of the nuclei in the aeciospore of a former eu-heteroecious *Puccinia*.

8. The confinement of certain unique genera like *Uromycopsis*, *Uromycladium*, *Ravenelia*, etc., to certain host families or genera indicates the probability of the early establishment and segregation of these rusts on particular branches of the phanerogamic tree. I wish to raise the question whether the wide gaps between the alternate hosts of certain rusts may not have been accentuated through the processes of evolution of the particular phanerogams which they inhabit?

9. The antithetic effects produced upon their respective hosts by the gametophyte of the rusts, which is evident in both autoecious and heteroecious species, indicate a primitive character as well as a

dimorphic condition of their ancestors, similar to that which HOWE has described for *Galaxaura*.

10. I conceive the rusts as originating from dimorphic red algae after the following manner. An endophytic tendency resulted in the gametophyte and sporophyte independently adapting themselves to whatever hosts were present. Postulating *Uredinopsis* as an ancient type, we may conceive of the independent sporophyte gaining a foothold in the ferns and the gametophyte establishing itself in the Abietineae. As parasitism became more fixed, the specialization to certain species of ferns and Abietineae became more complete, and heteroecism was established. I am thus in agreement with BLACKMAN regarding heteroecism as being a primitive character of the Uredinales. There appears to be no objection to supposing that in numerous cases both the gametophyte and sporophyte selected the same host, resulting in autoecism. In the light of such a hypothesis I can see no objection to deriving the short-cycle forms from long-cycle heteroecious and autoecious ancestors. The presence of correlated short-cycle forms of both heteroecious and autoecious species is our best evidence that such has taken place. The opsis and brachy types appear generally to represent intermediate forms between eu-autoecious species and their short-cycle micro and lepto-forms, since a number of such correlations are known. We should, therefore, search among the dimorphic red algae, and especially those forms which are parasitic, for evidences of the development of rust-like features, such as the basidium, the loss of sex organs, and a pleophagic condition of the alternate generations verging toward heteroecism.

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# A SECOND CASE OF MATERNAL INHERITANCE OF CHLOROPHYLL IN MAIZE[1]

M. DEMEREC

(WITH ONE FIGURE)

A character inherited only through the female gametes in maize has already been described by ANDERSON (1). He showed that the striped plants gave green, striped, and pale green progenies, whether pollinated with the pollen from the green or the striped plants. The green plants obtained from the striped ones gave only green progeny, the striped plants repeated the performance of the parent, and the pale green plants died. When seeds from striped plants were planted in the same order as found on the ear, the distribution of different types was not at random, but similar ones were grouped in patches. A test of pollen from striped plants showed that the character was not transmitted through the pollen. The case which will be described in this paper duplicates in all respects the inheritance of the character described by ANDERSON. It differs from it, however, by having an independent origin and a dissimilar phenotype.

## Material

The origin of the character dealt with in this paper was from a single variegated plant found by Professor C. B. HUTCHINSON in a field of Lucis Favorite maize grown for commercial purposes on Long Island. Seeds from this plant, which was open pollinated, were harvested when ripe, and given to the writer for genetical studies. A planting of these seeds made in the greenhouse gave 51 green, 26 pale green, and 48 variegated seedlings, among which last 3 were very light variegated (almost pale green), 26 light, 13 medium, and 6 very dark variegated. These results indicated that the newly found character might not be Mendelian in inheritance, so that the experiments were planned from the beginning in such a way as to test this hypothesis.

[1] Experiments reported in this paper were completed in the Department of Plant Breeding of Cornell University, Ithaca, New York.

### Description

Among the progeny of a variegated plant three kinds of seedlings may be found, green, variegated, and pale green. The pale green seedlings are typically expallescent, that is, in spite of having a large amount of chlorophyll they die in the early seedling stage (DEMEREC **15**). An analysis of the chlorophyll content was made according to the method described in this earlier paper, and it was found that pale green seedlings in three analyses made with different material had 46, 50, and 55 per cent of the amount of chlorophyll found in green plants of the same family. Pale green seedlings invariably died in approximately the same stage of development in which white seedlings die.

In the case of the variegated seedlings, if the green portions are small they die; but if the green portions are large enough for adequate production of food they develop into variegated plants. The amount of chlorophyll found in the pale green parts of the leaves decreases with the age of the leaf. Examination of a half-grown variegated plant shows that the upper leaves are pale green and green variegated, and that on the lower ones the pale green portions have become lighter and lighter, until they reach a yellowish white appearance, with little if any green color. A fully developed variegated plant looks like yellow and green, and not pale green and green variegated. A color determination was made on a variegated plant at the tasselling stage, using RIDGWAY'S (**27**) color standards, and it was found that green parts were elm green 27-m; and the pale green parts, from the upper leaves toward the lower, were as follows: light cress green 29″-i, lime green 25″, reed yellow 23″-b, and straw yellow 21′-d. A chlorophyll analysis of the leaves, taken from a variegated plant of the same stage, showed that the pale green portion of the upper leaf had 66.6 per cent and the pale green portion of the lower leaf 7.3 per cent as much chlorophyll as the green portions taken from the same leaves. So far as observed, the green seedlings always developed into green plants.

### Independence of maternal types

The surest and simplest method to establish a genetic difference for two Mendelian characters, which are phenotypically similar, is

to intercross them. In the case of characters which do not behave in the regular Mendelian way, however, this method fails. When deal-

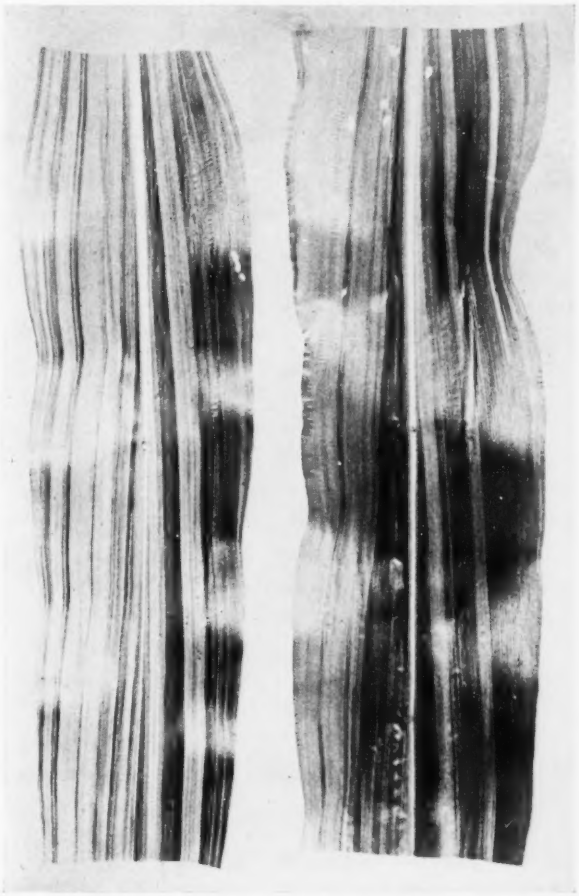

FIG. 1.—Leaves from variegated plant

ing with such characters, similar in effect, there is no way of determining with certainty whether they are genetically different or not.

In the present case it is possible to show that the maternal type described in this paper originated independently from the type de-

scribed by ANDERSON. This latter arose as a single plant, at Cornell University, in ANDERSON's cultures for genetic studies. On the other hand, the type dealt with in this paper was found as a single plant in a field of maize on Long Island, about 300 miles from Cornell. So far as known there is no evidence to indicate that the lines where these two types were found were ever intercrossed, or that the seeds have been mixed. This second maternal type was found in Lucis Favorite variety, which differs morphologically and in several known genetic characters from the variety in which the first maternal type was found. Subsequent breeding tests, carried on for several generations, showed that all progeny from the original ear taken from the first variegated plant were typically Lucis Favorite. This eliminated any possibility of intercrosses or mixture of seeds, and made it very probable that the two maternal types were independent in origin.

In addition to being independent in origin, the second maternal type also differs phenotypically from the first one. This difference is especially pronounced in the seedling state or in the young variegated plants. The pale green color of ANDERSON's maternal type is much lighter than that of mine. An analysis of the chlorophyll content made with the material, grown at the same time and under the same conditions, showed that the pale green seedlings of ANDERSON's maternal had 6 per cent of the normal chlorophyll, while the pale green seedlings of my maternal type had 46 per cent. A similar difference in the intensity of the pale green color can also be noticed on variegated plants when young. When variegated plants grow older that difference disappears, however, and both types look similarly yellow-white and green variegated. A photograph of the full grown variegated leaves of my maternal type is shown in fig. 1.

## Inheritance

TESTS OF FEMALE GAMETES.—As already mentioned, variegated plants produce three kinds of progeny, green, variegated, and pale green. Since the pale green plants die in the early seedling stage, only green and variegated plants could be used in the experiments to test the inheritance of the character.

PROGENY OF GREEN PLANTS.—So far as tested, green plants gave nothing but green progeny. From five different lines twenty-nine

green sibs of variegated plants were self-pollinated, and 4840 seedlings, grown from the seed of these plants, were examined. All of them were green, showing that the green plants did not transmit the variegation.

PROGENY OF VARIEGATED PLANTS.—Variegated plants rarely gave only green progeny, but usually produced pale green, variegated, and green progeny in varying proportions, irrespective of the

TABLE I

COMPARISON BETWEEN PROGENIES OF SELFED AND CROSSED SEEDS TAKEN FROM SAME EARS

| PEDIGREE NO. | PROGENY FROM | | | | | |
|---|---|---|---|---|---|---|
| | SELFED SEEDS | | | CROSSED SEEDS | | |
| | Pale green | Variegated | Green | Pale green | Variegated | Green |
| 613–19 | ..... | ..... | 115 | ..... | ..... | 3 |
| 617–30 | ..... | ..... | 70 | ..... | ..... | 4 |
| 617–27 | ..... | ..... | 65 | ..... | ..... | 3 |
| 613–22 | 0 | 3 | 104 | 5 | 11 | 11 |
| 613–5 | 11 | 15 | 46 | 18 | 10 | 14 |
| 613–7 | 63 | 20 | 15 | 61 | 14 | 17 |
| 617–1 | 190 | 27 | 14 | 23 | 11 | 3 |
| 613–10 | 186 | 7 | 3 | 25 | 2 | 5 |
| 459–2 | 139 | 8 | 2 | 5 | ..... | ..... |

kind of pollen used in fertilization. To determine the effect of the foreign pollen, the fertilization was brought about with a mixture of pollen from the variegated plant which was to be pollinated, and from some unrelated green plant which carried the dominant endosperm character present in the variegated plant in a recessive condition. On an ear pollinated by such a mixture of pollen it was possible by xenia to distinguish the seeds which were the result of self-pollination from those which came from the cross. This made it possible to determine on the same ear the effect of different male gametes on the progeny of a variegated plant. The data on the progeny of nine variegated plants pollinated with a mixture of pollen are given in table I, from which it can be seen that the male gametes did not influence the type of the progeny obtained. On individual ears the relation between the number of pale green, variegated, and green seedlings was practically the same from selfed and from crossed seeds.

Table II gives the progeny of sixteen variegated plants, which are arranged in three groups according to the intensity of variegation. From this table it can be seen that plants with large pale green areas are likely to give more pale green and variegated, and less green progenies, than plants where the pale green areas are very small. Some of the plants with few pale green stripes, however, gave

TABLE II

PROGENY OF VARIEGATED PLANTS

| PEDIGREE NO. | APPEARANCE OF ♀ PARENT | TYPE | | | PERCENTAGE | | |
|---|---|---|---|---|---|---|---|
| | | Pale Green | Variegated | Green | Pale green | Variegated | Green |
| 617–29 | Dark variegated (pale green parts take less than $\frac{1}{4}$ leaf area) | 0 | 0 | 80 | ..... | ..... | 100.0 |
| 617–29 | | 0 | 0 | 68 | ..... | ..... | 100.0 |
| 613–5 | | 29 | 25 | 90 | 20.2 | 17.4 | 62.4 |
| 617–10 | | 28 | 30 | 50 | 25.9 | 27.8 | 46.3 |
| 459–7 | | 55 | 79 | 76 | 26.2 | 37.6 | 36.2 |
| | Total | 112 | 134 | 364 | 18.4 | 22.0 | 59.6 |
| 617–30 | Medium variegated (pale green parts take $\frac{1}{4}$–$\frac{1}{2}$ leaf area) | 0 | 0 | 74 | ..... | ..... | 100.0 |
| 613–19 | | 0 | 0 | 118 | ..... | ..... | 100.0 |
| 617–30 | | 0 | 0 | 74 | ..... | ..... | 100.0 |
| 613–7 | | 124 | 34 | 32 | 65.2 | 17.9 | 16.9 |
| 617–1 | | 213 | 38 | 17 | 79.4 | 14.2 | 6.4 |
| 613–10 | | 211 | 9 | 8 | 92.5 | 4.0 | 3.5 |
| | Total | 548 | 81 | 323 | 57.5 | 8.5 | 34.0 |
| 613–22 | Light variegated (pale green parts take more than $\frac{1}{2}$ leaf area) | 5 | 14 | 115 | 3.7 | 10.4 | 85.9 |
| 613–23 | | 1 | 7 | 5 | 7.7 | 53.8 | 38.5 |
| 617–17 | | 29 | 43 | 21 | 31.2 | 46.2 | 22.6 |
| 459–2 | | 144 | 8 | 2 | 93.5 | 5.2 | 1.3 |
| 613–2 | | 25 | 0 | 0 | 100.0 | ..... | ..... |
| | Total | 204 | 72 | 143 | 48.7 | 34.1 | 17.2 |

relatively more pale green and variegated seedlings than those which had large pale green stripes, showing that the type of progeny does not always depend on the type of variegation of the parent plant. It is probable that the type of the progeny was determined by the type of tissue in the region where the ear was located, but no observations were made to prove this.

As in the case described by ANDERSON, it was found here also that the distribution of different types of seedlings with respect to their

position on the ear is not random, but that there was a tendency of like types to occur in patches. This can easily be observed by planting the seeds in approximately the same order as their location on the ear. Table III gives the results of one of the several plantings made. In this case the plant was pollinated with a mixture, and all seedlings resulting from cross-pollination are indicated in italics.

TABLE III

DIAGRAM OF EAR FROM VARIEGATED PLANT POLLINATED BY MIXTURE, GIVING APPROXIMATE POSITIONS OF SEEDS PRODUCING GREEN (*g*) VARIEGATED (*v*), AND PALE GREEN (*p*) SEEDLINGS; ITALIC TYPE INDICATES CROSS-POLLINATED SEEDS AND ROMAN TYPE INDICATES SELFED SEEDS

| SEED NO. | ROW | | | | | |
|---|---|---|---|---|---|---|
| | First | Second | Third | Fourth | Fifth | Sixth |
| 1 | *p* | v | *p* | *p* | *p* | p |
| 2 | *p* | *v* | p | *p* | p | p |
| 3 | *v* | v | p | *p* | p | *p* |
| 4 | *v* | p | *p* | p | *p* | p |
| 5 | p | p | p | *p* | *p* | p |
| 6 | p | *p* | p | p | *p* | *p* |
| 7 | *v* | v | p | p | *p* | p |
| 8 | p | v | *v* | *p* | *p* | p |
| 9 | *p* | p | p | *g* | *g* | p |
| 10 | p | p | *p* | *g* | v | p |
| 11 | v | *v* | *p* | *v* | v | *p* |
| 12 | *v* | p | p | *g* | v | p |
| 13 | v | *p* | p | *g* | *v* | *p* |
| 14 | *v* | p | *v* | *g* | v | p |
| 15 | p | p | *p* | *g* | v | *p* |
| 16 | p | *g* | *p* | p | v | *p* |
| 17 | *g* | *g* | *p* | p | *p* | p |
| 18 | *g* | *g* | *g* | *p* | p | *p* |
| 19 | *g* | *g* | *g* | *p* | v | p |
| 20 | ..... | *g* | *g* | *g* | *p* | *p* |

TESTS OF MALE GAMETES.—All experiments made with pollen from the variegated plants showed that the male gametes do not transmit the variegation to the progeny. With the pollen taken from nine variegated plants of different intensity, ten green plants were pollinated. The 651 $F_1$ plants were examined in the seedling stage, and 75 of them were grown to maturity, all being normally green. Fifty-six $F_1$ plants were selfed and 16,675 $F_2$ seedlings examined, and none of them was either variegated or pale green. Several ears segre-

gated virescent seedlings in a 3:1 ratio, however, showing that one of the parents brought into the cross a gene for virescent seedlings.

## Inoculation experiments

To test the possibility of the variegation being caused by a virus disease, inoculation experiments were made with young seedlings and with older plants. The method of inoculation was the same in both cases, namely, pale green leaves taken from the seedlings of the maternal line were rubbed thoroughly with the green leaves of the plant being inoculated. The injury done to the inoculated leaves differed on different plants, from a very slight to an extensive one. Inoculation by grafting was not tried, since grafting is rarely if at all successful in maize.

EXPERIMENT WITH SEEDLINGS.—About 350 green seedlings were inoculated at the four-leaf stage, and were kept in the greenhouse until the plants began to tassel. They were examined several times during their growth without any effect of the inoculation being noticed. All the plants, in all the stages at which the examination was made, were uniformly green.

EXPERIMENTS WITH MATURE PLANTS.—Mature plants were inoculated at the tasseling stage, inoculation being made on three leaves on each plant, namely, on the youngest and two of the older ones. In the experiment forty-four plants were used, seven of them being green sibs of variegated plants, and the remaining thirty-seven from crosses in which the male parent was a variegated plant. Careful examination of the inoculated plants was made several times, but no indication was observed of variegation being transmitted. From twenty-nine inoculated plants which were self-pollinated, 8576 seedlings were grown, and all of them were green.

## Conclusions

Experiments made to test the inheritance of this variegation showed that it is inherited only through the female gametes, and that the male gametes have no influence either on its transmission or its expression. All attempts made to transmit the variegation asexually were unsuccessful.

## Discussion

Among the characters affecting the development of chlorophyll in plants, many have been described which do not follow regular Mendelian inheritance. In regard to their transmission they can be divided into two groups (SHARP **28**), namely, characters having a maternal inheritance and those inherited biparentally.

Chlorophyll variegations inherited only through the female parent were described in *Antirrhinum* (BAUR **2**), *Arabis* and *Aubretia* (CORRENS **11**), *Glycine* (TERAO **33**), *Humulus* (WINGE **34**), *Hydrangea* (CHITTENDEN **6**), maize (ANDERSON **1** and the writer in the present paper), *Melandrium* (SHULL **29**), *Mesembryanthemum* (CORRENS **11**), *Mimulus* (BROŽEK **5**), *Mirabilis* (CORRENS **9, 10**), *Primula* (GREGORY **18**), and *Stellaria* (CORRENS **13**). Not completely tested, but probably belonging to the same group, are variegations described by CORRENS (**12, 13**) in *Hieracium*, *Mercurialis*, *Senecio*, and *Taraxacum*, and by KAJANUS (**21**) in *Pisum*.

The typical genetic behavior of the maternal variegations is as follows. (1) Seeds from the green branches of a variegated plant give green progeny, those from the pale green or white branches give pale green or white progeny respectively, and the seeds from the variegated branches give variegated, green, and pale green (or white) progeny in different proportions. (2) When a variegated plant is pollinated with the pollen from a green plant, the $F_1$ offspring do not differ from the offspring resulting from a selfing. (3) Pollen from the variegated plants does not transmit the variegation on $F_1$, $F_2$, or $F_3$ progenies.

In explaining the unusual inheritance of maternal variegations, CORRENS (**9, 10**) assumed that the character is not transmitted through the nucleus, since the sperm nucleus from the variegated parent does not transmit variegation, nor does the sperm nucleus from the green parent produce any change in the type of the progeny of a variegated plant. He thinks that the inheritance of these variegations is carried through the cytoplasm. With slight modifications, CORREN's hypothesis is almost universally accepted among geneticists. Some of them, however, are more specific than CORRENS in assuming that the bearers of inheritance in such cases are the plastids (GREGORY **18**, WINGE **34**, CHITTENDEN **6**).

An attempt was made by STOMPS (31) to explain such maternal inheritance on a chromosomal basis. The exceptional results, obtained in the reciprocal crosses between a maternal character and the type, he thinks have a parallel in certain crosses of species of *Oenothera*. Since the characters so inherited in *Oenothera* are assumed to be carried in the chromosomes, he does not see the need for another mechanism in explaining the heredity of maternal types.

In the case of maternal variegations, the experimental evidence in support of any of the explanations of their inheritance is not sufficient to be considered conclusive. There are no adequate $F_2$ data available from the cross between variegated female and green male. Such data obtained from the seeds grown from the light colored regions of variegated $F_1$ plants would complete the tests as to the effect of the male nucleus on the inheritance of these variegations. As the evidence stands now, it is possible to explain all of the observed facts by the assumption that the variegation is determined by a dominant mutable gene which has a highly increased frequency of mutations (as compared with the gene for the type), when it comes in contact with other than parental cytoplasm. Such a gene would become more mutable in the crosses between the type and variegated when the pollen from a variegated plant was used. If the rate of mutation from a gene for white or pale green to a gene for the type is high enough, the character would disappear in the early stages of development of the $F_1$ plants, and the young seedlings as well as the mature $F_1$ plants would be green, both somatically and genetically. On the other hand, in the case of the opposite cross (variegated ♀ by green ♂), the rate of mutation in the gene determining the character would not be increased, because the gene would be in the parental cytoplasm. Such a cross would be expected to give results similar to those obtained by self-pollination.

This maternal inheritance could also be explained by balanced lethals, as suggested by STURTEVANT (32). There is also a case in *Oenothera* described by KLEBAHN (22)[2] which duplicates the behavior of these maternal characters, and which would indicate that the nu-

[2] The writer is indebted to Dr. STURTEVANT for calling his attention to KLEBAHN'S paper.

clear mechanism not only could, but does account for the unusual behavior of characters inherited through the female gametes only.

As already mentioned, the experimental evidence does not justify a final conclusion on the mechanism for the inheritance of maternal variegations. In addition to the cytoplasmic explanation, there are several possibilities of explaining the observed facts on a chromosomal basis. It might be well to defer judgment as to which of the explanations is most probable, until more experimental evidence has been accumulated. The fact, however, that all known maternal characters deal with the development of chlorophyll, favors the non-Mendelian explanation, since it was shown by RENNER (**26**) and DAHLGREN (**14**) that chloroplasts may act as bearers of the inheritance of chlorophyll characters.

The variegation in *Pelargonium zonale*, which was genetically studied by BAUR (**2**) and NOACK (**24, 25**), is the only case described in which inheritance is biparental.[3] The variegation in *Capsicum annuum*, as described by IKENO (**19, 20**), might belong to the same group. Recent investigations, however, the results of which the writer learned from a conversation with Professor IKENO, indicate that the variegation in *Capsicum* is the result of an infectious disease.[4]

BAUR's data on the inheritance of *Pelargonium zonale* are given in table IV, from which it can be seen that the selfing of a *zonale* plant gave only white progeny; and in the $F_1$ generation of reciprocal crosses between green and *zonale*, green, variegated, and white offspring were obtained. To explain these results, BAUR suggested as a working hypothesis the possibility that the *zonale* character is inherited through the plastids. The tissue in the *zonale* plant from which the germ cells are formed has only white plastids, and therefore only white progenies are obtained by selfing. The results obtained in the crosses he explained by assuming that some plastids are brought into the fertilized ovum with the pollen nucleus. BAUR points out in his first paper on that subject (**2**) that his data are not sufficient for a

[3] The variegation described by RENNER (*25*) in *Oenothera* is considered to be different from that in *Pelargonium*, since it was shown that both nucleus and plastids are instrumental in the transmission of the character.

[4] The writer is much undebted to Professor IKENO for the permission to use his unpublished observations.

final conclusion. He gave his explanation as a working hypothesis for further research. BAUR'S explanation, however, has been accepted by the majority of the geneticists who have discussed the matter; and in his later presentations (3) BAUR himself is inclined to give more weight to the hypothesis than was originally intended.

STOMPS (30) suggested a Mendelian explanation for the behavior of *Pelargonium zonale*. He assumed that the character is determined

TABLE IV

BAUR'S DATA ON INHERITANCE OF PELARGONIUM ZONALE

| PARENTS | NO. OF CROSSES | $F_1$ PROGENY | | |
|---|---|---|---|---|
| | | Green | Variegated | White |
| zonale×zonale | 3 | ..... | ..... | 42 |
| white branch×green | 1 | 1 | ..... | ..... |
| green×white branch | 1 | 38 | 7 | 0 |
| green×zonale | 4 | 139 | 18 | 4 |
| zonale×green | 4 | 60 | 23 | 0 |
| zonale×white branch | 1 | ..... | ..... | 4 |

by a "perlabile pangene," not going into the details of the explanation. Extensive experiments with *P. zonale* were carried on by NOACK (23, 24, 25), who explains the inheritance of the character as follows:

> Als Arbeitshypothese wurde aus diesen Versuchen die Anschauung gewonnen, dass die Buntblättrigkeit der Schecken auf einer Stoffwechselkrankheit beruht, bei der Zellkern und Protoplasma in gleicher Weise beteiligt sein können. So kommt innerhalb der Meristemzellen eine Differenz in den Stoffwechselbeziehungen der beiden durch die Kreuzung vereinigten Partner zustande. Dieser labile Zustand kann durch gegenseitige Anpassung nach der einen oder anderen Seite in einen irreversiblen Zustand überführt werden, und dadurch entstehen rein grüne bzw. rein farblose Keimlinge oder Zweige, oder aber er kann zu einer Art Gleichgewichtszustand zwischen gesundem und krankem Elternanteil führen, und daraus resultieren dann Mantelchimären der verschiedensten Art. Es handelt sich somit bei diesen ganzen Erscheinungen nicht mendelnder Buntblättrigkeit keineswegs um einen Fall echter Vererbung, sondern um eine einfache Übertragung eines mehr oder weniger reversiblen Krankheitszustandes auf die Nachkommen.

In the material used by NOACK, sterility prevented selfing and crosses between *zonale* plants. He succeeded in obtaining only eight seeds from such pollinations, all of which gave white seedlings, con-

firming BAUR'S results. Reciprocal crosses with green, when a *zonale* plant was used as female, gave besides green progenies a larger or smaller number of variegated plants and a few white seedlings; when the green was a female parent very few variegated plants were obtained. In this respect NOACK'S results differed from those obtained by BAUR. Green $F_1$ plants gave always green progeny when intercrossed, and in the crosses with *zonale* behaved as other green plants. An important contribution of NOACK is the discovery that different *zonale* plants give different proportions of variegated plants in crosses with green, and also that the type of variegation was different in the progeny of the different plants. Certain plants gave a progeny with large proportions of white tissue, while the variegated progeny of other plants had very small white areas. The majority of the variegated seedlings became green in the later stage of development, some of them became white and died, and only a few remained variegated throughout life.

The important facts from BAUR'S and NOACK'S results may be summarized as follows: (1) *Zonale* plants selfed or intercrossed gave white progeny only. (2) In crosses with green plants, white, variegated, and green $F_1$ seedlings were obtained in varied proportions. According to BAUR, reciprocal crosses gave like results, but in the case of the material used by NOACK a larger proportion of variegated plants was obtained if *zonale* was the female parent. (3) Green $F_1$ plants, as well as green portions of variegated plants, behaved in $F_2$ and crosses as normal green. (4) In crosses with green, different *zonale* plants transmitted the variegation in different proportions and intensity.

The data so far obtained do not give sufficient support to either BAUR'S hypothesis or NOACK'S. Results identical with those obtained in the experiments would be expected if it is assumed that the *zonale* character is determined by a dominant gene which becomes mutable (mutating to the gene for green) in crosses with green, or when the plant is heterozygous for green. Such an assumption would be supported by similar behavior observed in several other cases. EMERSON (17) found that the mutability of the gene for variegated pericarp is much increased when the gene is in the heterozygous condition. When maize with very light variegated (almost

white) pericarp was crossed with white pericarp, in the $F_1$ generation white, variegated, and red seeds were obtained. CORRENS (**7, 8**) had a similar experience with variegated *Mirabilis*. In the case of the mutable character, miniature wing, found by the author in *Drosophila virilis* (data not yet published), an almost constant miniature becomes highly mutable at the maturation division in the presence of a dominant autosomal factor, and in the presence of another factor becomes very mutable in somatic cells. Reddish, another mutable character known in *Drosophila virilis* (**16**), mutates only when heterozygous. The fact, observed by NOACK, that reciprocal crosses between *zonale* and green gave different results, could be explained by the assumption that the mutability of the gene for white is increased when brought by the pollen nucleus into other than maternal cytoplasm. Such an assumption is warranted, judging by the results obtained from the studies on mutable genes in *Drosophila* (data not yet published), which indicate that the environment of the gene has an influence on its mutability.

The available data already stated are not adequate to show the validity of the mutable gene hypothesis. The hypothesis, however, is susceptible of some simple tests. If the *zonale* character is determined by a dominant gene for white (W) which becomes mutable when heterozygous (Ww), then the white sectors on the variegated $F_1$ plants from the crosses *zonale* by green are expected to be Ww. Flowers located on these Ww sectors crossed with pollen from green plants ww are expected to give half of the progeny of the constitution ww, which would be green, and the other half of the constitution Ww, which would be white, variegated, or green. The same flowers in crosses with *zonale* (WW) are expected to have half WW (white) progeny and half Ww (white, variegated, or green); and when selfed one-quarter of the progeny should be WW (white), one half Ww (white, variegated, or green), and one-quarter ww (green). The results from these and similar crosses would be expected to show enough difference to permit a conclusion as to the validity of the hypothesis.

It is well to keep in mind that certain virus diseases produce cholorophyll abnormalities similar in appearance to characters described as being non-Mendelian. Some of the diseases could be trans-

mitted in such a manner that they might easily be mistaken for a heritable character (BLAKESLEE 4). To reduce the possibility of such a mistake to a minimum, thorough inoculation experiments seem obligatory before reaching the conclusion that a character is non-Mendelian.

## Summary

1. A chlorophyll variegation is described which is inherited through the female parent only. A variegated plant gives pale green, variegated, and green progeny in varying proportions, irrespective of the kind of pollen used in fertilization.

2. A similar character was already described by ANDERSON. The present one, however, in addition to having an independent origin, differs phenotypically from that previously described.

3. All attempts to transmit the character asexually by inoculation were unsuccessful.

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# CHROMOSOME STUDIES IN AESCULUS[1]

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(WITH PLATES III–V)

For several seasons the writer has been studying the pollen formation in *Aesculus*. For the most part, the material for this study has been collected at the Arnold Arboretum and at the Harvard Botanic Garden. The buds were killed in chrom-acetic acid (0.7 per cent), and in Carnoy's fluid, imbedded in nitro-cellulose, and stained in Haidenhain's iron-alum haematoxylin with either safranin or eosin as a counter stain.

The genus *Aesculus* is not a large one, although quite well distributed throughout the Northern Hemisphere. By far the best known species is the common horse-chestnut, *Aesculus hippocastanum* L., which was introduced into the United States about 1746 (1). A microscopic examination of the developing anther shows conditions which are essentially normal. There is slight indication of irregularity in the movement of the chromosomes during meiosis, but it is very rare and not at all pronounced. Moreover, the pollen grains are seldom morphologically imperfect. In other words, from the standpoint of cytology, this form appears to be specific in rank, and is generally considered so by systematists. Hybrids between this species and some red-flowered American buckeye, probably *Aesculus pavia* L. (1), are quite commonly used for ornamentation. Of these *A. rubicunda* Lois. (*A. carnea* Hayne) is perhaps the best known. An examination of the pollen development in this form shows features common to known hybrids. It and the next type (*A. rubicunda* var. *brioti* Carr.) are the only ones studied which show more than twenty chromosomes after reduction. Here we find forty chromosomes as the haploid number, so that the form is tetraploid. During meiosis lagging chromosomes appear frequently. While still held within the mother cell, five or six pollen grains are often present instead of the usual number of four. One of these pollen grains (two,

[1] Contribution from the Department of Biology, Williams College.

if six are present) is much smaller than the rest, and undoubtedly gives rise to the not infrequent small and shriveled pollen grains which are found in the mature anther. In fig. 1 is illustrated the chromosomes arranged at the cell plate during the second (homotypic) division, and one can easily count the forty present. The divisions appear quite regular. In fig. 2 nearly the same stage is shown in another pollen mother cell. The chromosomes in the plate view are not all present, some being cut out of the section, but those in the other spindle, which appears in side view, show a distinct tendency to lag. Figs. 3 and 6 illustrate polyspory as present in the above. Note in fig. 3 the gigantic pollen grain together with four small ones. This condition is not so common as that shown in fig. 6. Doubtless the gigantic grain is just as useless as are the small ones. Fig. 4 illustrates in *A. rubicunda* var. *brioti* how conditions like those shown in fig. 6 are probably developed. Here the second (homotypic) division of the mother cell is illustrated. One of the main spindles shows distinct lagging of chromosomes, but the point of chief interest is the extra spindle. This has doubtless arisen from chromosomes which have dropped off the main spindle in the first (heterotypic) division, and have formed a small spindle of their own. Such a phenomenon has often been noted in cytological work done on other genera (**6, 31, 32, 33, 52,** etc.), and is the usual cause for polyspory. Fig. 8 shows the mother cell of the same variety undergoing the reduction division, and the lagging chromosomes are plainly visible. Fig. 7 illustrates the mature stage of the variety *brioti*, and shows the great difference in size between morphologically good and morphologically sterile pollen grains.

*A. hippocastanum* var. *baumannii* Schneider is a double flowered variety supposedly of *A. hippocastanum* L. REHDER suggests that the irregularity of chromosome behavior in this form may not be due to hybridization, but to the influence which brings about the doubling of the flowers, and he advocates taking up the whole question as to the cause for the doubling of flowers. Be that as it may, the chromosome irregularities are very suggestive of hybridity. Fig. 9 shows the plate view of two spindles during homotypic division. It will be noted that the haploid number is twenty, as is apparently the case with all species except *A. rubicunda* Lois. and *A. rubicunda*

var. *brioti*. In fig. 10 is shown what is apparently one spindle during the homotypic division. It will be seen that certain chromosomes are small and seemingly double, while others are large and single. This phenomenon cannot be observed in most species, nor do individual chromosomes vary markedly in shape and size as they do in many plants and animals. Fig. 11 is a somewhat later stage during the heterotypic division. Figs. 12, 13, and 15 illustrate the mature pollen grains yet held in the mother cell. In no case was the writer able to observe polyspory, but there seems to be a marked irregularity in the number and size of grains in each mother cell. Another interesting fact is that often whole pollen sacs appear to degenerate, the pollen mother cells becoming vacuolated and empty, and sometimes irregular tapetal-like cells become greatly enlarged and fill the whole sac.

*A. glabra* Willd., a common tree of the Mississippi Valley, appears perfectly normal in its meiosis, and hence is a good species from the cytological point of view. Two of its so-called varieties, however, proved interesting. *A. glabra* var. *buckleyi* Sarg., a form found growing in certain localities in Missouri, Iowa, and Kansas, shows a very large proportion of sterile pollen grains. Unfortunately the writer was unable to procure any of the early stages of development, and so cannot report upon the chromosome behavior. *A. glabra* var. *leucodermis* Sarg. is a tree reaching 18–20 m. in height, and is characterized by having five-foliolate leaves, yellow flowers, and pale smooth bark. An examination of the chromosomes during meiosis showed distinct lagging during the heterotypic division, and slight irregularities during the homotypic division. In the mature stage a small percentage of morphologically sterile pollen grains appears.

*A. arguta* Buckley is considered by systematists a closely related species to *A. glabra* Willd. It is a "small narrow shrub tree-like in habit," found growing naturally in Oklahoma and a few localities in northern and central Texas. Here we find distinct lagging of chromosomes in the first division, as shown in fig. 28. The chromosomes are more normal in the homotypic division, and yet there is also some irregularity. In the mature stage there is a large percentage of morphologically sterile pollen.

*A. octandra* Marsh (Sweet buckeye), also called *A. flava* Ait., grows as a large tree or shrub in rich woods from western Pennsylvania northward to Wisconsin, westward to Iowa, and southward to Georgia, Alabama, and Texas. Its pollen development shows no irregularity to indicate that the plant is not of specific rank. One tree, however, labeled *A. octandra* and growing in the Harvard Botanic Garden, gave strong evidence of being a hybrid. There was a large number of sterile pollen grains at maturity, and lagging of chromosomes was plainly evident in the reduction division. Fig. 23 shows the situation during heterotypic division, when the majority of chromosomes have arrived at the plate preparatory to dividing. The lagging of chromosomes is quite evident. In fig. 26 a later view is shown, after the majority of the chromosomes have divided and passed to the poles. It will be seen that one pair of chromosomes is distinctly behind the rest, and that still another chromosome is slow in joining with the general group.

One form, known as *A. octandra* var. *hybrida* (DC) Sarg. and characterized by having purple or red flowers, is found growing along the Alleghany Mountains from West Virginia southward and westward. This is considered by REHDER as a hybrid between *A. octandra* Marsh. and *A. pavia* L. Sections of this form show one of the best examples observed of polyspory. In fig. 20 such a pollen mother cell is illustrated. It will be seen that there are seven pollen grains of varying sizes visible. Lagging is also in evidence during the heterotypic and homotypic divisions. Fig. 21 illustrates such lagging in the homotypic division. Only one division is shown, since the other was largely eliminated from the section by the microtome knife. Because the writer was unable to obtain any mature stages, the situation with regard to morphologically sterile pollen could not be studied. However, one would expect to find the sterile grains abundant.

As already stated, *A. flava* Ait. is considered by systematists a synonym for *A. octandra* Marsh. The *A. flava* studied in this article was collected at the Harvard Botanic Garden, and from the standpoint of the pollen formation certainly behaves like a hybrid. Fig. 24 illustrates lagging during the heterotypic division, when the majority of chromosomes have arrived at the cell plate. Fig. 27 shows a stage similar to fig. 24, but during the second division.

Lagging of chromosomes may clearly be observed. In fig. 18 the mature pollen grains appear. These are largely degenerated and nearly empty of protoplasm.

The form *A. discolor* Pursh was apparently first discovered in Lyon, Georgia. As first described, it is a shrub not more than about four feet high with "leaflets tomentose on lower surface and flowers yellow, white and purple, variegated." The description has caused much confusion. In 1824 DE CANDOLLE referred it to his *A. hybrida*, believing it to be a hybrid between *A. lutea* (*octandra*) and *A. pavia* L. In 1828 TORREY and GRAY made a variety *discolor* of *A. pavia* L., to which they doubtfully referred the plants of PURSH, LINDLEY, and DE CANDOLLE. Later GRAY made this plant a variety *purpurascens* of *A. flava* Ait. SARGENT believes *A. discolor* Pursh to be a true species (45). One variety, *A. discolor* var. *mollis* n. var., found growing in Georgia and Alabama, has bright scarlet flowers. In fig. 25 is illustrated the heterotypic division in this variety, and it will be seen that lagging is in evidence. In the mature stage considerable morphological sterility of pollen is also present.

Another form, *A. octandra* var. *discolor* Rehder, very closely related if not identical with *A. discolor* Pursh, also shows lagging chromosomes during the heterotypic and homotypic divisions, and many sterile pollen grains are present at maturity. Fig. 22 gives evidence of the lagging during heterotypic division. It will be noted that one pair of chromosomes is especially slow in reaching the plate.

*A. harbisonii* Sarg. is a late flowering variety considered to be a hybrid between *A. discolor* var. *mollis* n. var. and *A. georgiana* Sarg. It is a rare shrub with "rose-colored calyx and canary yellow petals tinged with rose toward the margin." Further proof for its hybrid origin appears when a cytological study of its pollen formation is carried out. It shows excellent examples of lagging during the heterotypic division, and less commonly during the homotypic division. In fig. 30 the heterotypic division is portrayed, and it will be seen that a large number of chromosomes are slow in reaching the plate of the spindle. In fig. 29 the homotypic division is illustrated, and one pair of chromosomes will be observed to be slow in arriving at the equator of the spindle. The mature pollen sac does not show a large amount of morphologically sterile grains, but there are always some present.

*A. georgiana* Sarg. was first discovered near Stone Mountain in Georgia, but has since been found to range into the Piedmont region of North Carolina, where it becomes a small tree. It has been given specific rank by SARGENT. From the cytological standpoint it appears to be of hybrid origin. In fig. 19 the chromosomes are shown well arranged for counting, and it will be observed that there are twenty. In fig. 17 it will be seen that there is plenty of lagging during the heterotypic division. In fig. 16 five pollen grains are shown held within their mother cell. One grain distinctly smaller than the rest lies directly over a larger one. At maturity a large proportion of morphologically sterile pollen grains are present.

In fig. 5 the heterotypic division of *A. mutabilis* var. *induta* n. hyb. Sarg. is shown. This form is considered a hybrid by the systematists, and it will be seen that cytological evidence during the heterotypic division bears out this viewpoint. Lagging chromosomes are also present to some extent during homotypic division, although not so common. *A. mutabilis* var. *pendulifolia* Sarg. is also considered to be a hybrid. Its parents are thought to be *A. discolor* var. *mollis* n. var. and *A. neglecta* Sarg., also considered to be a hybrid. Lagging of chromosomes is abundant in this form during heretotypic division, and many sterile pollen grains appear at maturity.

*A. woerlitzensis* Koehne, E. is a form of unknown origin which came first from Europe. Cytologically it appears to be a hybrid, showing plentiful lagging of chromosomes in the heterotypic division and a large proportion of sterile pollen at maturity.

## Discussion

The literature on meiosis in plants makes clear that much study has been given the subject, and that many different points of view have arisen. Every student of botany is acquainted with normal meiosis, at least in the vascular plants, and knows that all research on the subject has furnished increasing proof that each species of plant, under normal conditions, has a constant number of chromosomes, and that species closely allied to each other tend to have the same, or nearly related chromosome counts.

In the majority of cases meiosis is perfectly regular. It is not with the normal condition that the great interest lies, however, but with certain irregularities which are discussed in this article.

We usually find in the life history of a vascular plant a continuous cycle of alternation between the sexual (haploid) and non-sexual (diploid) phases of the individual. There is now an increasing list of examples where this is not the case, and where by one of a variety of ways the alternation is broken. Such phenomena are listed under the heading of apomixis, and, although not noted in *Aesculus*, are known to be often the result of hybridization.

Another extremely interesting variation, and one which at the present time is occupying the attention of cytologists, is the occurrence of an increased number of chromosomes. Whereas in most plants each genus has a definite gametophytic (haploid) number of chromosomes in the reproductive cells, examples are increasing where certain species of the same genus may have instead the number increased sometimes as high as ten times the original. These polyploid forms, in which the number of chromosomes is some multiple of the regular haploid number common to the genus in question, are often spoken of as euploid (**52**). On the other hand, certain genera, as for example *Carex* (**14**), show among their various forms chromosome numbers which are greater than the haploid number but which are not a multiple thereof. Such a condition is known as aneuploid. JEFFREY (**21**) has suggested the terms artiploid, perissoploid, and dysploid instead of the preceding, for the forms respectively where the chromosome numbers are even (diploid, etc.), uneven (triploid, etc.), and where the number does not come under the law of multiples (*Carex*, *Crepis*, etc.).

Along with polyploidy, although frequently also where the chromosome number is not increased, one often finds that certain chromosomes lag behind during meiosis, and either eventually catch up with the others to enter into the structure of the daughter nuclei, or become cast off into the surrounding cytoplasm. In many cases these laggards appear to be univalent and hence slower in their movements, but in certain cases the univalents appear to move faster than the bivalents, and consequently there seems to be no fixed rule.

When chromosomes lag behind and are extruded into the cytoplasm, they may degenerate or they may form spindles of their own during the second meiotic division, and develop small excess nuclei. These nuclei may degenerate or may become the center of small

pollen grains, which, added to the usual number of four, cause an increase in the number in each mother cell. Such small grains usually do not reach maturity but become shriveled and empty (polyspory).

ERNST (9), ROSENBERG (41), WINGE (57), TÄCKHOLM (52), and others believe hybridization to be one of the most common, although not the only cause for sterility in plants and animals. Many artificial crosses have been carried out and much morphological sterility has been observed. Along with this sterility apomixis and lagging chromosomes, as well as polyploidy and polyspory, may occur. In the now classic *Drosera* cross of ROSENBERG (39) it is definitely shown that when these two species of different chromosome numbers (*D. longifolia* with twenty in the haploid and *D. rotundifolia* with ten in the haploid) are crossed, the resulting hybrid shows ten bivalent and ten univalent chromosomes. The latter lag behind the former, especially in the heterotypic division. The lagging chromosomes are often extruded into the cytoplasm, and form small spindles from which extra pollen grains are developed.

Since this investigation many similar ones have been made. In his investigation with *Oenothera* crosses, GATES (11, 12, 13, etc.) has found many aberrations similar to those found in *Drosera*, and suggests that "irregular tetrad-formation puts under suspicion the purity of any plant in which it is found." DIGBY (8), working with *Primula* hybrids, was able to obtain tetraploid offspring. YASUI (59) and LJUNGDAHL (30), studying *Papaver* hybrids, found very interesting irregularities. TISCHLER (54, 55), in his results with *Ribes* and *Bryonia* hybrids, observed such irregularities as lagging chromosomes, polyploidy, and polyspory. Likewise in the work of SAKAMURA (44), and more recently of KIHARA (26, 27, 28, 29) and of SAX (46, 47, 48) with *Triticum* hybrids, these irregularities also often appear.

Several years ago JEFFREY (20) pointed out that there are many natural hybrids in existence which, while propagating themselves and breeding more or less true, are nevertheless hybrids in origin (crypthybrids). Many of these are known to propagate themselves either by purely vegetative means or through apomixis, but there are others which are forming enough viable seeds to greatly increase their number. One at once wonders why such plants which should

be heterozygous do not segregate out. Certain geneticists have attempted to answer the point by supposing the presence of so-called "balanced lethal" factors which make the plant appear as a heterozygote. Whether this explanation is the right one or not seems hard to determine, but in any case such hybrids have long given the taxonomist great trouble in determining the proper classification of the plants in question.

Recently much study has been given these natural hybrids, and very interesting results have been obtained. The Rosaceae have long been known to have several genera which show great irregularities. In 1916 Miss COLE (**7**) showed through a study of various species of *Rosa* that much sterility of pollen is present. The studies of TÄCKHOLM (**52**), BLACKBURN and HARRISON (**6**), and PENLAND (**37**) have revealed much about the cause for this condition. They find great irregularities, such as polyploidy, polyspory, lagging chromosomes, and apomictic phenomena. The writer (**15**) showed the presence in *Rubus* of much morphological sterility of pollen. LONGLEY (**32**) cleared up the situation and showed meiotic peculiarities closely resembling those recorded for *Rosa*. Miss STANDISH (**51**) reported much sterility in pollen in the very unsettled genus *Crataegus*, and later LONGLEY (**33**) also showed the situation here to be similar to that for *Rosa* and *Rubus*. Among the Compositae, TAHARA (**53**) and ISHIKAWA (**18**) for *Chrysanthemum*, ROSENBERG (**41**) for *Hieracium*, ROSENBERG and others (**42**) for *Crepis*, and HOLMGREN (**16, 17**) for *Erigeron* and *Eupatorium*, have found similar peculiarities. The work of HEILBORN (**14**) with *Carex* is extremely interesting. In *Carex*, as already mentioned, there is a wide range of chromosome numbers, forming a large series of aneuploid types, and together with this polyploidy occur other irregularities so commonly found in hybrids. Finally, JEFFREY and HICKS (**23, 24**) have recorded an apparent hybrid form of *Isoetes*, found growing in Cape Breton Island, which shows two types of chromosomes (large and small). The small appear constantly to lag behind the large. This form also shows an extreme sterility. The authors also report a very abundant lagging of chromosomes in the Boston fern. This is known to be a very sterile form propagating by vegetative methods. If we accept the hybrid origin of this fern as fact, and it seems hard not to when

one takes into consideration how it originated as well as its chromosomal irregularities, it is easy to understand why so many clones appear, as reported by BENEDICT (3, 4, 5).

In the preceding paragraphs an attempt has been made to show that the irregularities recorded in certain plant genera are common to both artificial and natural hybrids; therefore when such irregularities, or some of them, appear in certain forms of *Aesculus* they put the purity of their ancestry under suspicion.

## Conclusions

*Aesculus* gives abundant proof, in addition to that already obtained through work done upon *Rosa*, *Crataegus*, *Rubus*, *Oenothera*, and other plants, that chromosome irregularities and morphological sterility of pollen are usually present in known hybrids, and thus, when found in plants of uncertain origin, are indicative of hybrid ancestry.

Since the chromosome count in most forms of *Aesculus* shows twenty chromosomes present in the reduced stage, it would not be expected that the pollen formation would present as many irregularities as in a genus like *Rubus*, where polyploidy has been found as high as the octoploid number. However, chromosome irregularities and morphologically sterile pollen are abundant in *Aesculus*.

A study of the pollen formation in *A. hippocastanum*, *A. glabra*, and *A. octandra* gives additional evidence that these forms should be considered of specific rank. Likewise plants such as *A. rubicunda*, *A. rubicunda* var. *brioti*, *A. octandra* var. *hybrida*, *A. harbisonii*, *A. mutabilis* var. *induta*, and *A. mutabilis* var. *pendulifolia*, which are considered hybrids by systematists, appear to be such when the pollen formation is taken into consideration. *A. woerlitzensis*, a form whose origin seems to be uncertain, is apparently a hybrid.

When the pollen formation of the other varieties of *Aesculus* is considered, the results appear to be more or less at variance with the opinion of the systematists. *A. hippocastanum* var. *baumannii*, considered by the systematists a variety of *A. hippocastanum*, shows marked irregularity in pollen formation. *A. glabra* var. *buckleyi* and *A. glabra* var. *leucodermis*, considered varieties of *A. glabra*, show many of the irregularities of hybrids. *A. arguta*, considered as a

species closely allied to *A. glabra*, has plentiful lagging of chromosomes and an abundance of morphologically sterile pollen at maturity. *A. flava*, considered as another name for *A. octandra*, at least in the material studied, shows plenty of evidence for a hybrid origin. The variety *mollis* of the supposed species *A. discolor* has lagging chromosomes and morphologically sterile pollen. *A. octandra* var. *discolor*, a form possibly identical with *A. discolor*, in chromosome behavior and in sterility of pollen appears to be of hybrid origin. Finally, *A. georgiana*, named by SARGENT and considered by him of specific rank, not only shows lagging chromosomes and sterile pollen, but also polyspory.

*A. rubicunda* and *A. rubicunda* var. *brioti* are of special interest, since their chromosome count after the heterotypic division is forty; hence they must be ranked as tetraploid.

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## EXPLANATION OF PLATES III–V

Magnification of figures 1400 unless otherwise specified.

FIG. 1.—*A. rubicunda* Lois.: section of pollen mother cell during homotypic division, showing chromosome count of forty.

FIG. 2.—*A. rubicunda* Lois.: section of pollen mother cell during homotypic division, showing lagging of chromosomes.

FIG. 3.—*A. rubicunda* Lois.: mature pollen mother cell, showing irregularity in size of pollen grains; one grain gigantic in size and others small and nearly empty.

FIG. 4.—*A. rubicunda* var. *brioti* Carr.: section of pollen mother cell during homotypic division, showing lagging of chromosomes in one spindle and small third spindle formed from chromosomes dropped from spindle during heterotypic division.

FIG. 5.—*A. mutabilis* var. *induta* n. hyb. Sarg.: section of pollen mother cell during heterotypic division, showing lagging of chromosomes.

FIG. 6.—*A. rubi unda* Lois.: mature pollen mother cell showing polyspory; four of pollen grains normal in size while other two are dwarfed.

FIG. 7.—*A. rubicunda* var. *brioti* Carr.: mature pollen grains showing empty grains mingled with those normal in appearance; ×700.

FIG. 8.—*A. rubicunda* var. *brioti* Carr.: pollen mother cell during heterotypic division, showing lagging of chromosomes in spindle.

FIG. 9.—*A. hippocastanum* var. *baumannii* Schneider: pollen mother cell during homotypic division, showing chromosome count of twenty.

FIG. 10.—*A. hippocastanum* var. *baumannii* Schneider: pollen mother cell during homotypic division (only one spindle), illustrating lagging of chromosomes (note that some chromosomes appear paired).

FIG. 11.—*A. hippocastanum* var. *baumannii* Schneider: pollen mother cell during heterotypic division showing chromosomes arriving at equator of spindle with some lagging behind.

FIGS. 12, 13, 15.—*A. hippocastanum* var. *baumannii* Schneider: pollen mother cells with pollen grains already formed, showing irregularity in number and size of grains.

FIG. 14.—*A. hippocastanum* var. *baumannii* Schneider: homotypic divisions of pollen mother cell showing marked lagging of chromosomes in both spindles.

FIG. 16.—*A. georgiana* Sarg.: section of pollen mother cell showing polyspory.

FIG. 17.—*A. georgiana* Sarg.: section of pollen mother cell during heterotypic division showing lagging of chromosomes.

FIG. 18.—*A. flava* Ait.: mature pollen grains showing contrast between morphologically sterile and perfect pollen grains; ×700

FIG. 19.—*A. georgiana* Sarg.: section of pollen mother cell during heterotypic division, showing chromosome count of twenty.

FIG. 20.—*A. octandra* var. *hybrida* (DC) Sarg.: section of pollen mother cell showing polyspory.

FIG. 21.—*A. octandra* var. *hybrida* (DC) Sarg.: section of pollen mother cell during heterotypic division, showing lagging chromosomes.

FIG. 22.—*A. octandra* var. *discolor* Rehder: section of pollen mother cell during heterotypic division showing lagging of chromosomes.

FIG. 23.—*A. octandra* Marsh. (?): section of pollen mother cell during heterotypic division showing lagging of chromosomes.

FIG. 24.—*A. flava* Ait.: section of pollen mother cell during heterotypic division showing lagging of chromosomes.

FIG. 25.—*A. discolor* var. *mollis* n. var.: section of pollen mother cell during heterotypic division showing lagging of chromosomes.

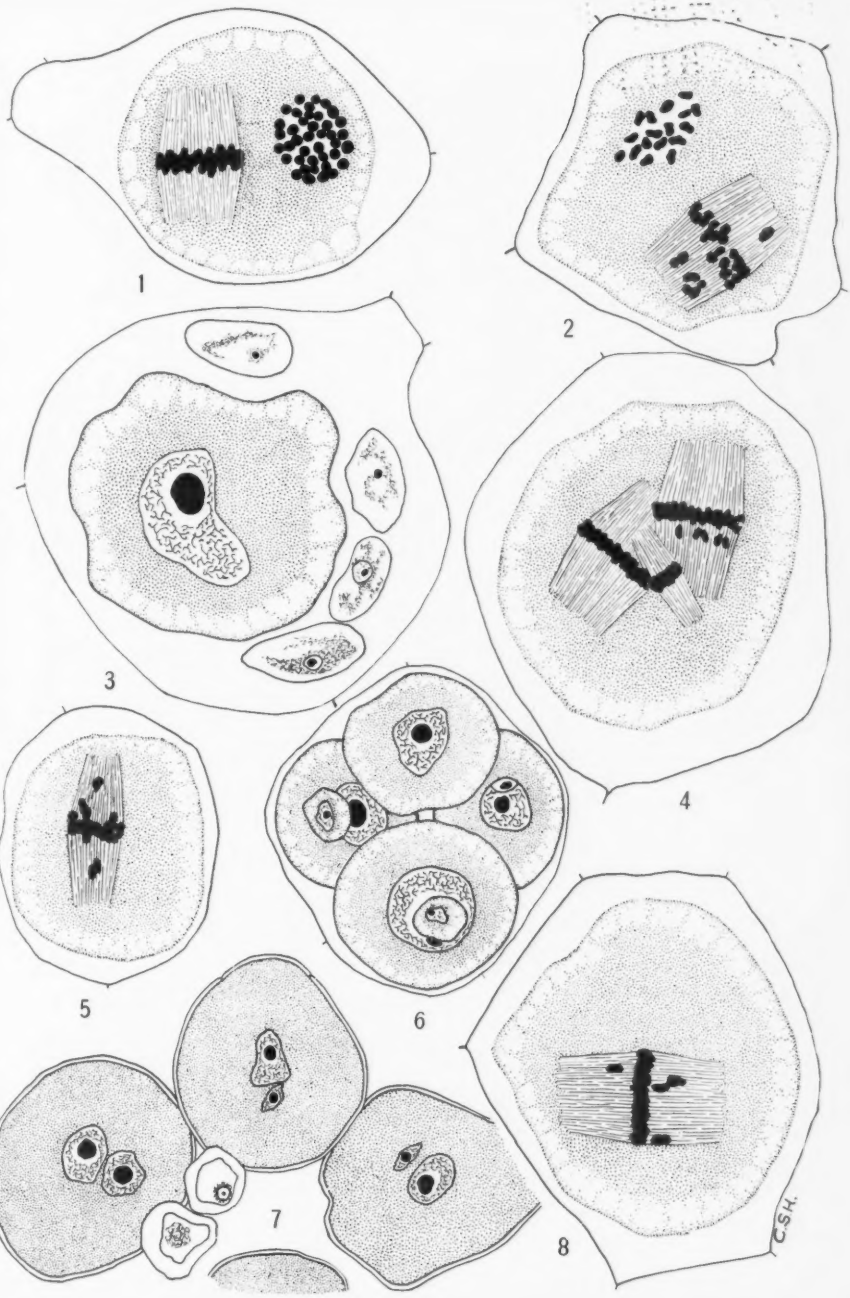
FIG. 26.—*A. octandra* Marsh. (?): section of pollen mother cell during heterotypic division (later stage than shown in fig. 23), showing distinct lagging of one pair of chromosomes.

FIG. 27.—*A. flava* Ait.: section of pollen mother cell during homotypic division showing lagging chromosomes.

FIG. 28.—*A. arguta* Buckley: section of pollen mother cell during heterotypic division showing lagging of chromosomes.

FIG. 29.—*A. harbisonii* Sarg.: section of pollen mother cell during homotypic division showing lagging of chromosomes.

FIG. 30.—*A. harbisonii* Sarg.: section of pollen mother cell during heterotypic division showing lagging of chromosomes.

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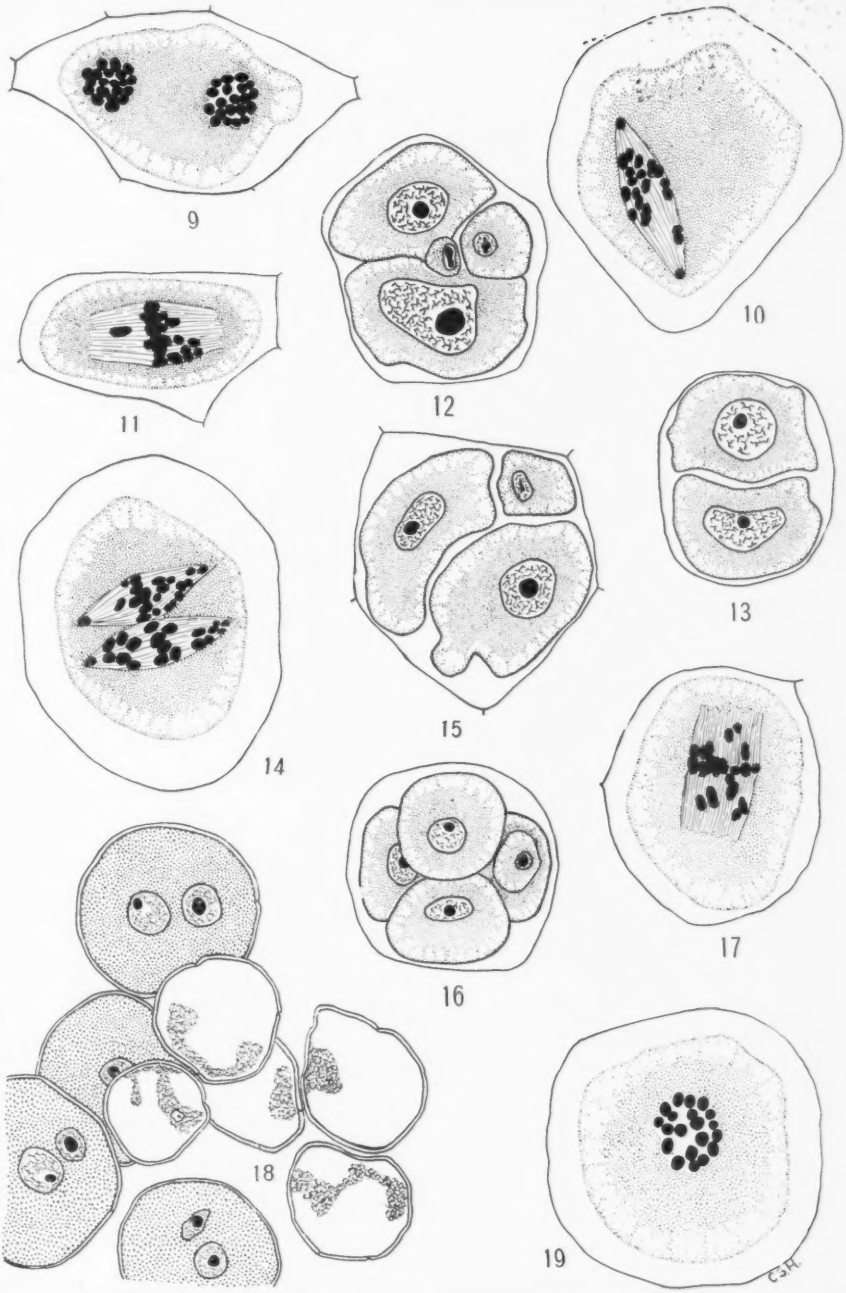


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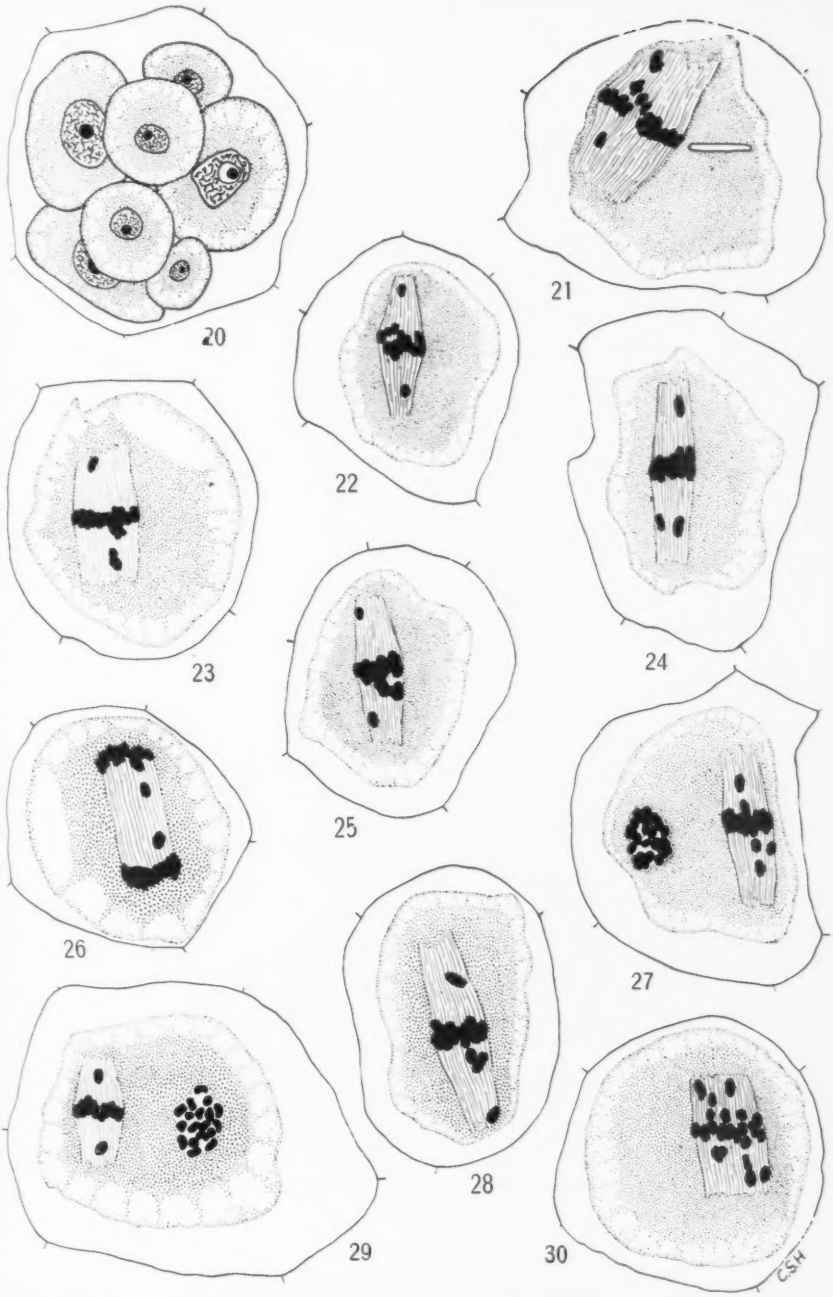



HOAR on AESCULUS

# CYTOLOGICAL STUDIES IN THE GENUS WISTERIA[1]

MURIEL V. ROSCOE

(WITH PLATE VI AND SIX FIGURES)

Frequently vines of Asiatic *Wisteria* in cultivation are entirely given over to vegetative development and never produce flowers or fruit. Both the Asiatic and American species present varying degrees of pollen sterility. This study was undertaken to see whether any morphological basis for these conditions could be found.

## Materials and methods

The collection of *Wisteria* at the Arnold Arboretum contains most of the varieties of the Asiatic and American species. The buds used were obtained chiefly from this source. Additional material of *W. sinensis* was obtained from the Botanic Gardens of Harvard University, as well as from privately owned vines. Collecting was confined to warm days and was carried on only in the middle of the day.

The buds were cut with a sharp razor and put immediately into the fixing fluid. Both chromo-acetic (0.75 per cent) and Carnoy's solutions were tried as fixatives, and the results were found to be superior after the Carnoy's. The air was exhausted by means of an air-pump. After fixing and subsequent washing, the buds were softened and bleached in a 10 per cent solution of a saturated solution of sodium chlorate in hydrofluoric acid. Then after thorough washing and gradual dehydration in alcohol, they were imbedded in nitrocellulose. Extensive use was made of the mass method for nitrocellulose, originated by JEFFREY (20). The sections were cut at thicknesses of 5 and 10 $\mu$, and stained in Haidenhain's iron-alum haematoxylin. For pollen study, safranin was used as a counter stain.

The sections were studied with the assistance of a 1.5 mm. Zeiss apochromatic objective and nos. 5 and 12 compensating oculars. All

[1] Contribution from the Laboratories of Plant Morphology, Harvard University.

text figure drawings were made with the aid of a Spencer camera lucida, used in conjunction with the 1.5 objective and 12 ocular, and were reduced one-half in photographing. The figures of the plate are free-hand drawings, but are accurate representations and give magnifications of approximately 1500.

The nomenclature used for the species and varieties obtained from the Arnold Arboretum is in accordance with the labeling of the plants there, while I am indebted to Professor C. S. SARGENT for furnishing the authorities for these names. For the identification of *W. sinensis* gathered from other sources, use has been made of BAILEY'S manual (1).

## Observations

### ASIATIC SPECIES

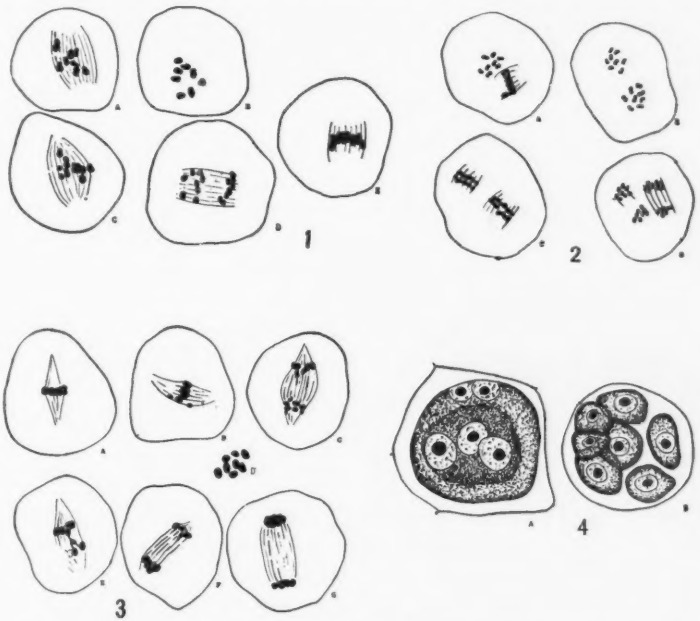
*W. floribunda* DC., var. *macrobotrys* Rehder & Wilson, $\times = 8$.—All phases of both the heterotypic and homotypic divisions manifest regularity. The tetrads formed show no suggestion of polycary or polyspory, yet the mature pollen rarely exhibits more than 75 per cent of perfect grains.

*W. floribunda* DC., var. *alba* Rehder & Wilson, $\times = 8$.—The behavior of this variety showed a deviation from the regularity noted for var. *macrobotrys*, particularly in regard to the metaphase of the first division. Fig. 1 *A* and *C* may be considered representative of the condition which obtains if the chromosomes are "caught" on their way to the plate, and the relation of the chromosomes to the spindles is comparable with that shown in hybrid meioses. Despite a lack of concerted action in heterotypic anaphase (fig. 1 *D*), apparently all the chromosomes become included in the daughter nuclei. In the homotypic division (fig. 2 *A–D*) the abnormalities are negligible, and the tetraspores are formed in the usual fashion. However, mature pollen sacs disclose only about 45–50 per cent of protoplasmic pollen grains.

*W. floribunda* DC., var. *rosea* Rehder & Wilson, $\times = 8$.—The material was not sufficient to furnish a clear idea of the progress of the divisions. Unimbedded material showed 75–85 per cent of the pollen in young buds to be fully protoplasmic.

*W. sinensis* Sweet, $\times = 8$.—Fig. 7 shows diakinesis with 8 bivalent chromosomes, a highly vacuolated nucleolus, and a fine, loose

network of threads. The chromosomes show some tardiness in forming the metaphase plate, but usually they all arrive there before the beginning of anaphase. The separation of the halves of the bivalents, and a transition to anaphase are indicated in fig. 8. Interkinesis is of some duration and is featured by abundant nucleoli, as




FIGS. 1–4.—Fig. 1, *W. floribunda* var. *alba*, heterotypic divisions: *A*, early metaphase; *B*, metaphase (polar view); *C*, early metaphase; *D*, anaphase; *E*, metaphase; fig. 2, *W. floribunda* var. *alba*, homotypic divisions: *A*, *B*, metaphase; *C*, *D*, anaphase; fig. 3, *W. sinensis*, meiotic abnormalities occurring in pollen mother cells of midsummer buds: *A*, *B*, *D*, metaphase; *C*, *E*, *F*, anaphase; *G*, telophase; fig. 4, *W. venusta: A*, polycary; *B*, polyspory showing 7 microspores formed from one pollen mother cell.

many as 4 (fig. 11) being frequently observed. The meaning of the conspicuous masses of black-staining material in the cytoplasm is vague. Tetraspores resulting from the homotypic division all show complete normality in their early stages (fig. 13), and degeneration occurs only later.

The pollen grains often remain in masses, and frequently are unable to form an exine coat. In other cases the grains develop walls, but become crumpled and lose their protoplasmic contents. At most, but 60–65 per cent of viable grains mature (fig. 5).

Fig. 3 shows the irregularities observed in buds of the midsummer flowers of *W. sinensis*. Fig. 3 *B* illustrates a frequent condition; *C*, *E*, and *F* picture various anaphases characterized by abnormality with chromatin spread along the spindle fibers. In some cases such chromatin actually bridges the gaps between chromosomes (*E*, *F*). Telophases of a normal character are occasionally achieved (*G*). In these divisions abnormality is very much the rule, but in spite of this at least a few good pollen grains are formed, and some of the late flowers frequently set seed. Although the figures seen in the spring flowers may scarcely be called irregular, neat plates are rarely attained in *W. sinensis*, and in the summer flowers the abnormalities of meiosis are very conspicuous.

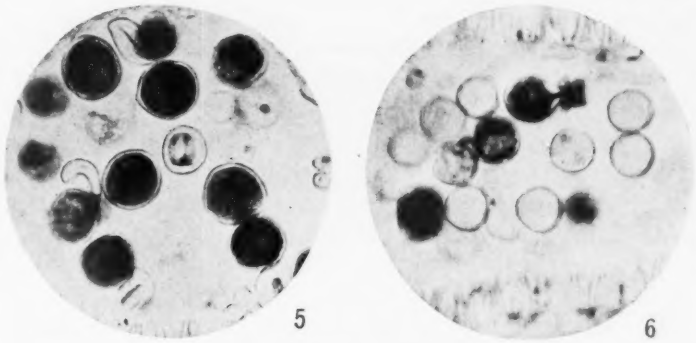
*W. venusta* Rehder & Wilson, $\times = 8$.—Heterotypic stages differ little from those recorded for *W. sinensis*. The amount of material containing homotypic telophases was small, but in this, one decided case of polycary with five nuclei was found (fig. 4 *A*). A large number of locules revealed microspores in the tetrad stage and many cases of polyspory. As many as 7 spores were observed as resulting from a single pollen mother cell (fig. 4 *B*). Until a study of more material of homotypic divisions showing distribution of the chromosomes is possible, no conclusions are warranted in regard to the appearance of polycary and polyspory in this species. The pollen shows a very high percentage of sterile grains, of which many are conspicuously small. Probably very few are capable of effecting fertilization.

### American species

*W. macrostachya* Nutt., $\times = 8$.—The material did not disclose sufficient division figures to allow of any conclusions. The microspores appear to be formed in tetrads, no cases of polyspory having been observed. In a few cases the tetraspores seemed unable to separate from one another. Cytomixis takes place frequently, and has been seen to occur between daughter tetraspores of different pollen mother cells. The pollen contains almost no good grains.

*W. frutescens* (L.) Poir., var *alba* Rehder & Wilson, $\times = 8$.—This proved to be the only variety of the American species containing satisfactory stages for detailed study. The figures disclose nothing very different from the chromosome relations expressed in the Asiatic species. In diakinesis the chromosomes are clearly bivalents, and the heterotypic division apparently proceeds normally.

Although the material containing the homotypic stages was collected only in chromo-acetic, and consequently showed the chromo-




FIGS. 5–6.—Fig. 5, *A*, pollen of *W. sinensis;* c. 600×; fig. 6, pollen of *W. frutescens* var. *alba;* c. 600×.

somes massed together at the plates, there was no indication of anything but regularity of chromosome distribution. In those tetrads examined, no case of polycary or polyspory presented itself. The pollen proved very sterile, only a few grains in a locule appearing normally protoplasmic (fig. 6).

## Discussion

FIXATIVES.—Buds fixed in Carnoy's fluid and in chromo-acetic solution gave very different results. Sections containing the pollen mother cells show more shrinkage after Carnoy fixation than do those preserved in chromo-acetic. In contrast with chromo-acetic treatment, following Carnoy's the chromosomes show no tendency to clump; consequently ideal sections for counting are obtained. Thus whenever the Carnoy material provided the desired stages, this

alone was studied, and chromo-acetic-fixed material was resorted to only when absolutely necessary.

An interesting comparison of the two fixatives is in their effect on the perinuclear zone. This zone has been observed to be omnipresent in *Wisteria* cells during division, and may be found also in the young tetrads. Its significance is not at all apparent, although it seems similar to the "perikaryoplasm" in *Cobaea scandens* described by LAWSON (**26**), and to such zones as occur in cotton (CANNON **6**) and the Cucurbitaceae (CASTETTER **8**). The nature of the zone seems to have been modified by the fixative used. After Carnoy's, this zone is most definite in extent and is strongly contrasted externally with the cytoplasm and internally with the clear nuclearplasm, while after chromo-acetic its outer and inner limits are not sharply set off, and often it is found to have invaded the spindle. DEVISÉ'S observations (**11**) on *Larix* led him to conclude that the felted perinuclear zone is an artifact produced by the fixing fluids. Those fluids containing large amounts of acetic acid modified that part of the cytoplasm surrounding the nucleus with its contained particles to give a felted appearance.

Black-staining masses are of frequent occurrence in the cytoplasm in all the *Wisteria* preparations, but they are more conspicuous in those fixed in chromo-acetic. For a study of the chromosomes and their relationships, Carnoy's proved to be a suitable fixative.

NUCLEOLI.—WILSON (**40**) discusses nucleoli as being of two sorts, plasmosomes and karyosomes, and considers their origin "still to a considerable extent in doubt; but the evidence is accumulating that all forms of them may be directly derived from the chromosomes."

The nucleolus seen in prophase of *Wisteria* divisions takes a very dark haematoxylin stain, but just previous to the dissolution of the nuclear membrane at the close of diakinesis, it becomes highly vacuolated and reacts less strongly to haematoxylin (fig. 7). The appearance suggests that there is a relation between the nucleolus and chromatin.

After the first division, two, three, or more nucleoli appear, and frequently are formed before the chromosomes have lost their morphological individuality, and thus before the nucleus can be said

to have become organized for the resting period. The correlation between chromatin and nucleoli is not as clear as in the prophase.

CYTOMIXIS.—In *Wisteria macrostachya*, cytoplasmic strands were seen connecting pollen mother cells at various stages of development, chiefly at synizesis but also even between formed tetraspores. The presence of this phenomenon at so late a stage is rare in plants, for mention of it in the literature is usually confined to synapsis stages.

HETEROTYPIC AND HOMOTYPIC DIVISIONS.—The roses are divided by TÄCKHOLM (**37**) into three major groups: (1) In which normally only paired chromosomes appear during the reduction division. Here are contained diploid, tetraploid, hexaploid, and octaploid species and hybrids. (2) In which both paired and unpaired chromosomes appear, but in multiples of seven. The Caninae constitute this division. (3) In which the chromosomes are not in multiples of seven. Forms with such a constitution are termed aneuploid hybrids, and originated by the hybridizing of Canina roses. The first group contains diploid species and hybrids, which are the forms of interest in relation to *Wisteria*.

TÄCKHOLM considers the diploid hybrids are either long-cultivated hybrids with uncertain histories, or forms which have arisen spontaneously, or the products of known crossings. A strong affinity exists between the chromosomes of such hybrids, and there is little disturbance in the divisions of the pollen mother cells. This investigator found the course of meiosis regular, and the tetrads and even the young pollen grains looked usually entirely normal. The mature grains were not studied.

Of the known crosses, *R. chinensis*×*multiflora*, the "Dawson rose," shows no deviations from the normal in meiosis, and the young microspores appear of similar size and health after they have rounded off. Similarly, in *R. microphylla*×*rugosa* only occasionally is the affinity weakened in one of the seven pairs, and metaphase, anaphase, and telophase usually show no disturbance; only in a few cells among hundreds is a separate chromosome found lying free in the plasma.

A very comparable situation is found in *Wisteria*, where the history is also one of long cultivated forms which quite possibly have

arisen as a result of crossings. In these the fundamental chromosome number is eight, and, as in *Rosa*, there is a strong affinity between the homologous chromosomes. Thus the chromosomes of the forms investigated always appear as bivalents in diakinesis and go on the spindle as such.

BLACKBURN and HARRISON (5) examined *Salix* to discover if possible whether variability was of the same sort as in *Rosa*. Diploid, tetraploid, and hexaploid species were found, but in only three cases were abnormalities in meiosis manifested; these were in *S. fragilis*, *S. aurita*, and *S. andersoniana*, and even here the abnormalities were not great. Although they were not so glaring as those characterizing the Rosae, the irregularities were such as to suggest hybridity. Three recognized *Salix* hybrids were examined: *S. viminalis*×*S. purpurea*=*S. rubra* Sm. and *S. caprea*×*S. lanata* gave no disturbance of any sort, not even abortion of pollen grains; while the third, *S. aurita*×*S. phylicifolia*, showed irregular heterotypic division with micronuclei and an irregular homotypic division. In spite of these conditions, the tetrads of the latter cross are not defective and never exceed four in number. Only later is there degeneration resulting in sterile pollen. These investigators thus note that irregularities do not need to be great to suggest hybridity, and the hybrids, *S. viminalis*×*S. purpurea* and *S. caprea*×*S. lanata*, show also that crossing without resulting chromosomal disturbance may occur; while, as shown in *S. aurita*×*S. phylicifolia*, anomalies in division do not preclude the formation of the normal number of microspores, even though sterile pollen may eventually develop.

CANNON (7) very early studied hybrids between different races of peas. Apparently the parents in this case were not very dissimilar, for these race hybrids were fertile, matured their spores regularly, and no abnormal mitoses were observed.

LONGLEY (27, 28, 29) has reported variability associated with polyploidy for *Rubus* and *Crataegus*. This author in a recent paper on *Citrus* (30) finds variability to be general among cultivated diploid forms, and in reference to the variability despite lack of polyploidy in *Citrus*, *Iris*, *Zea* and their relatives, he says: "It seems probable that this variability is the outcome of long cultivation where selection and hybridization would naturally occur." It occurs

to the writer that species of *Wisteria* have been subjected to the same features of selection and hybridization.

The well known work of ROSENBERG (**34**) on *Drosera obovata* has shown this form to be a hybrid between two parents of different chromosome number, and the resulting chromosomal action is quite unlike anything observed in *Wisteria*.

JÖRGENSEN (**24**), discussing the chromosome composition and behavior of Danish species of *Callitriche*, decided that hybrids between types with similar chromosome numbers usually do not form dwarf nuclei. This is obviously the condition which obtains in *Wisteria*, and if further investigation on *W. venusta* discloses the chromosomal constitution to be eight, it will form an interesting exception to *Callitriche* conditions, since *W. venusta* divisions frequently allow the formation of more than 4 microspores.

Two *Crepis* crosses involving *C. biennis* (with 20 haploid chromosomes[2]), *C. setosa* (with 4 haploid chromosomes), and *C. capillaris* (with 3 haploid chromosomes) were studied by COLLINS and MANN (**10**). The cross with the greatest discrepancy in chromosome numbers gave fewer irregularities than the one where a difference of only one chromosome existed, and these authors reported the following conclusion:

> Since the $F_1$ of *C. setosa* (N=4)×*C. capillaris* (N=3) shows very abnormal reduction phenomena while *C. setosa*×*C. biennis* reduces almost normally, it is evident that normality of reduction does not depend upon similarity of chromosome number, but rather upon likeness of internal composition of the chromosomes.

WINGE (**41**), in a review of chromosome numbers, reports 8 and 12 as occurring most frequently. To the long list of plants already reported as having 8 chromosomes must now be added various species of *Wisteria*. Concerning hybrid organisms, WINGE says:

> Among plants, specific hybrids are as a rule sterile; indeed, imperfect pollen formation in flowering plants may often be a criterion of their hybrid origin (JUEL 1901 and others) . . . . On the whole, imperfect reduction is associated with the hybrid nature.

If WINGE'S supposition is correct, we might very readily believe from the sterile pollen in *Wisteria* that here we have hybridized

[2] ROSENBERG (**36**) gives the somatic count for *C. biennis* as 42.

species which have arisen presumably as a result of the propinquity of like-chromosomed parents.

POLYCARY AND POLYSPORY.—*W. venusta* represents the only *Wisteria* species in which polycary and polyspory were observed. There are on record numerous cases where one or both of these phenomena appear in the development of microspores, and in zoological material cases of polyspermy have also been discovered. BEER (**2, 3**) found supernumerary pollen grains in *Fuchsia* and these resulted from irregular divisions; also he noted a definite relation between the number of chromosomes entering a nucleus, the size of the nucleus, and the size of the cell produced.

Among the Rosaceae, BLACKBURN and HARRISON (**4**) in their study of *Rosa* counted as many as 8 pollen grains which originated from one mother cell. TÄCKHOLM (**37**) illustrated a similar condition for *R. canina allodonta*. PENLAND (**32**) figured polycary in *R. alberti*, and as many as 7 microspores, one binucleate, formed in *R. rubrifolia;* while ROSENBERG (**33**) gives 10 microspores as resulting from one pollen mother cell. LONGLEY (**28, 29**) showed polyspory in *Rubus* and in *Crataegus*.

Illustrations of these conditions may be had in *Crepis* hybrids (COLLINS and MANN **10**), in *Hemerocallis* (FULLMER **13**), in *Nicotiana* (GOODSPEED **14**), in *Callitriche* (WINGE **41**), etc. HOLMGREN (**17**) shows that as many as 10 nuclei may be formed from one pollen mother cell in the anthers of peripheral flowers of *Eupatorium glandulosum*.

As noted by JÖRGENSEN (**24**) for *Callitriche*, the small microspores are usually the first to degenerate, and it is rare that they are able to effect fertilization; indeed they usually perish by the time the shedding stage is reached, and make their contribution to the sterility of pollen. Thus polyspory explains the higher percentage of sterile pollen in *W. venusta* than in the other Asiatic species of *Wisteria*.

The work of the investigators mentioned, and also that of many others (TISCHLER **39**; JEFFREY, LONGLEY, and PENLAND **22**; LONGLEY **30**) makes it apparent that polyspory is the result of irregular chromatin distribution in one or both divisions, and this has come to be regarded as an accompaniment of hybridism.

POLLEN STERILITY.—WULFF (43) considered sterile pollen in plants to be (1) the result of hybridization; (2) an accompaniment of mutation; (3) the results of other influences (temperature, light intensity, moisture, and soil). Of these, hybridization was the most common cause. Since mutating forms have been shown to exhibit cytological phenomena similar to those characterizing hybrids (JEFFREY and HICKS 20, 21; JEFFREY and ROSCOE 23), the first two causes given by WULFF may be considered as one.

TISCHLER (38) concluded that "die Pollensterilität kein Specificum des Bastards ist," but one or both parents used in the crossings of *Mirabilis*, *Potentilla*, and *Syringa* which he studied contained sterile pollen, and in the case of *Potentilla* this was accompanied in one parent (*P. tabernaemontani*) by abnormal meiosis; hence comparisons between them and their offspring in regard to pollen sterility cannot well be made. Nor is it necessary to decide that, because the percentage of sterile pollen is increased by subjecting the plants (parents and hybrids) to adverse physiological conditions, pollen sterility, when it occurs in these forms growing under normal circumstances, is not a significant feature.

Reference has been made repeatedly by investigators working with hybrid material, both plant and animal, to the sterility of pollen and of sperms produced. The causal relationship between meiosis and sterility has further been described (WODSEDALEK 42; ROSENBERG 35; TÄCKHOLM 37; HOAR 16; LONGLEY 28, 29; BLACKBURN and HARRISON 4; BEER 2).

HARRISON'S (15) opinion that sterility is the result of latent hybridity is in accord with the ideas expressed by JEFFREY (18, 19) and his students (FORSAITH 12 and COLE 9).

From the evidence which we now possess, it seems logical to conclude that when plants growing under normal environmental conditions produce a high percentage of sterile pollen, the explanation may be looked for in previous crossing.

If *Wisteria* species are diploid hybrids, as has been suggested as a possible hypothesis, then despite the apparent compatibility of the chromosomes during meiosis, it seems that sterility may be due to the qualitative differences of the parental chromosomes.

## Conclusions

The evidence thus far obtained suggests that *W. venusta*, inasmuch as polyspory is common in the species, may be a somewhat anomalous *Wisteria*. If the supernumerary microspores have been formed here as a result of irregular chromosome distribution, it is probable that they contain fewer than 8 chromosomes, but a study of further material is necessary before any conclusions can be reached. The larger flowers of this form and its vegetative hardiness with the earlier flowering, as well as the additional factors of polycary and polyspory (since these are characteristics common among plants which have resulted from crossings), excite suspicion that *W. venusta* has been derived by hybridization.

Apart from the species just discussed, it has seemed reasonable to compare *Wisteria* with diploid rose hybrids, and with *Salix* hybrids in which crossing has not caused any chromosome disturbance. In the latter genus such hybrids may be entirely fertile. The cross *Salix aurita*×*S. phylicifolia* is even more nearly analogous, for here we have normal microspore formation but eventually sterile pollen.

The genus has been shown to disclose no inconsistency in chromosome numbers. On the contrary, the number seems to be invariably 8. Diakinesis, whenever examined, reveals always 8 pairs constituting firm bivalents, without any suggestion of a loose union of the elements. Any tardiness in reaching the plate, or in the subsequent separation of the chromosomes, is insufficient to cause inequality of the distribution of these units. The action of the chromosomes, however, as for example in *W. floribunda* var. *alba*, displays the sort of tardiness seen in meiotic divisions of hybrids. It is believed that the lack of promptness manifested here is due to the dissimilarity of the elements constituting the bivalents.

Coupled with the chromosome behavior is the still further factor of sterile pollen. Such conclusions as those of MEEHAN (31), who thought there was not "any more sterility attached to hybrids than to ordinary plants," have long since been abandoned.

From the behavior of the chromosomes during the meiosis of the pollen mother cells, and from the presence of varying degrees of sterile pollen, the conclusion is reached that the genus *Wisteria* contains hybridized species.

**Summary**

1. *Wisteria* pollen mother cells show a perinuclear zone which is more conspicuous after Carnoy fixation than after chromo-acetic.

2. Carnoy's fluid proved preferable for a study of the chromatic figure.

3. Toward the close of prophase the nucleolus becomes vacuolated and loses its intensely basophylic nature.

4. At interkinesis usually more than one nucleolus appears, and three and four are frequently formed.

5. The fundamental chromosome number in *Wisteria* is eight.

6. All the species and varieties examined, both Asiatic and American, show this haploid number.

7. Meiosis proceeds for the most part regularly, although frequently a lack of prompt chromosome action is apparent; this is particularly noticeable in *W. floribunda* var. *alba*.

8. Normal tetraspore formation occurs except in *W. venusta*, where conditions of polycary and polyspory are frequently developed.

9. Asiatic species show varying percentages of pollen sterility. Of these, *W. venusta* develops the highest number of non-functional grains.

10. American species show large amounts of pollen sterility. Comparatively few of the grains reveal cytoplasmic content.

11. *W. venusta* is considered on the basis of polycary, polyspory, and pollen sterility to be of hybrid origin. Other *Wisteria* species with varying degrees of sterile pollen are considered analogous to diploid hybrids in *Rosa* and *Salix*.

12. Pollen sterility is explained as arising from the qualitative differences of the parental chromosomes.

These investigations have been carried on under the direction of Professor E. C. JEFFREY, and I wish here to express my sincere appreciation of his unfailing interest and assistance.

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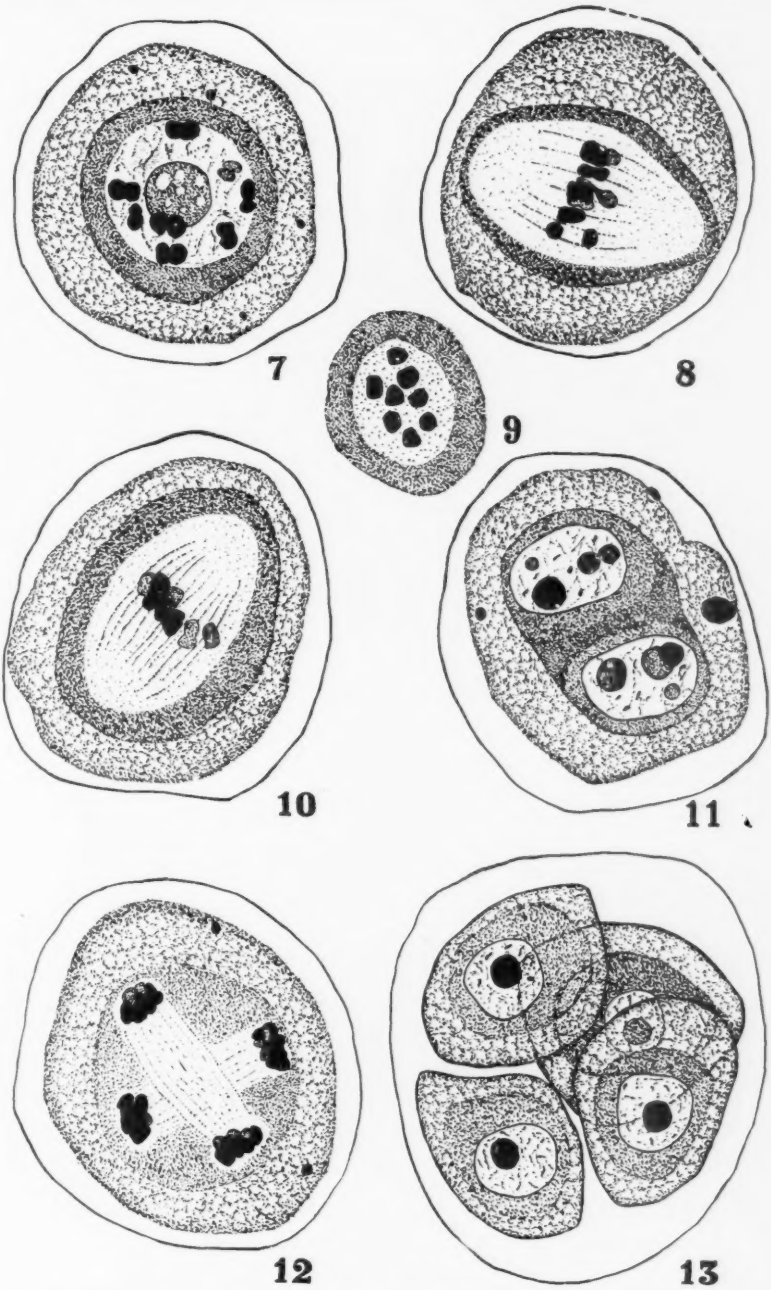
## EXPLANATION OF PLATE VI

*W. sinensis* Sweet: pollen mother cells during meiosis; magnification approximately 1500.

FIG. 7.—Diakinesis, showing 8 bivalents.
FIG. 8.—Beginning of heterotypic anaphase.
FIG. 9.—Polar view of heterotypic metaphase.
FIG. 10.—Heterotypic metaphase.
FIG. 11.—Interkinesis, showing abundant nucleoli and cytoplasmic masses.
FIG. 12.—Homotypic telophase.
FIG. 13.—Tetraspores.




ROSCOE on WISTERIA

# ANATOMY OF SEEDLING BUDS OF QUERCUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 373

LaDema Mary Langdon

## Introduction

(WITH PLATES VII–IX)

To the present time investigators of the vascular anatomy of the genus *Quercus*, or allied genera, have confined their attention in their search for evidences of conservatism chiefly to the radical, transition region and cotyledonary node of the seedling, or to details of vascular organization in the first annual ring, leaf, node, and root of the adult plant. In these accounts very few and brief are the references to the manner of origin and development of the vascular tissues of the vegetative organs. Believing that an explanation for certain problems relating to nodal anatomy in this genus is more likely to be found in a study of the seedling than in further investigation of mature portions of the plant, the present study of the anatomy of seedling buds has been undertaken. An attempt has been made to determine, for at least two species of *Quercus*, the exact manner of origin, and the course and relation of the vascular elements of the bud scales, leaves, and stipules, so well demonstrated in seedling buds with their close nodal formation; also, in so far as possible, to ascertain the origin of the primary tissues of the stem and the general features of shoot formation.

## Material and methods

As a basis for the major part of the investigation, seedlings of *Quercus alba* and *Q. rubra* one to four weeks old, with epicotyls ranging from 1.5–5 cm. in length, have been selected, and serial sections, both transverse and longitudinal, secured through tip portions of the seedlings in such a manner as to include both terminal and axillary buds. For a better understanding of tissue development in the stem, earlier stages in germination (either shortly before or directly after

the emergence of the plumule from the testa and pericarp) were obtained.

The seedlings which furnish the basis for the greater part of this study were from seeds procured in the outlying districts of Chicago, Illinois, the seeds being germinated and the seedlings grown in the botanical greenhouse of the University of Chicago. The preparation and study of the preserved material has been carried out chiefly at Goucher College, Baltimore, and at the botanical laboratory of the Johns Hopkins University.

In dealing either with seedling or winter buds of *Quercus*, great difficulty is likely to be experienced in the preparation of the material, owing to the close overlapping bud scales and numerous glandular hairs on the young stem and foliage leaves. Serial celloidin sections were tested but found to be inferior to paraffin sections where fineness of detail was desired. The seedlings were imbedded in paraffin in the usual manner, care being taken to exhaust all air from tissues before imbedding, thus insuring more perfect infiltration. Sections were then made, either with a rotary microtome or, where dealing with especially refractory tissues, a Spencer sliding microtome. By the latter method a complete series was obtained, by removing each section as cut from the knife, and arranging sections in series upon a slide well coated with albumen fixative and flooded with water. This method has been described in detail in a previous paper (10). Sections were cut 8–10 $\mu$ thick. Safranin and light green and Flemming's triple stain were used, the latter combination proving more satisfactory in the differentiating of meristematic tissues.

A typical terminal bud of a seedling, either of *Quercus alba* or *Q. rubra*, consists of several bud scales, numerous stipules, young foliage leaves, and leaf primordia. The stipules may occur as leaflike appendages arising from either side of the bases of the leaf petioles, or they may occur in pairs without the associated lamina. The latter condition, as pointed out by GOEBEL (4), is occasioned apparently by the arrested development of the lamina of certain of the outermost leaves whose stipules serve as protective organs. Three interesting stages are represented in these seedling buds in the transition from bud scales, which correspond in their development merely to the leaf bases of the more highly segmented foliage leaves, to

foliage leaves where the primordium preserves its normal size and shape. The arrangement and mode of connection with the central cylinder of the vascular elements of the outer paired stipules and bud scales have given rise to two types of nodal structure seldom, if ever, associated with *Quercus*, "unilacunar" and "bilacunar" nodes.

**Stem tip**

The origin of tissues at the growing point of leaf stems of angiosperms has been the object of numerous investigations, the conclusions from which in the main are contradictory. Literature on this subject dating to 1890 has been so carefully reviewed by DOULIOT (2), that only a brief summary is necessary here, chiefly of works relating directly to the group under discussion. To 1890, according to DOULIOT, one might place in one of two groups authors who had contributed to or concerned themselves with terminal growth in the stems of angiosperms, first those who observed in these plants a single initial cell, and second those who distinguished two or three distinct "histogens."

HOFMEISTER (8), the first to describe an initial cell at the summit of an angiosperm, reported a unique initial in *Zostera marina*, this cell being visible at the beginning of development where it divides as the terminal cell of *Equisetum*. He cited later (9) the maple and ash as having a cuneiform terminal cell, most of the other trees as having a tetrahedronal cell. In 1869 PRINGSHEIM (11) reported a single terminal cell at the stem tip of *Utricularia*, and in 1877 NAEGELI maintained that the leaf of *Elodea* developed, like that of the Cryptogams, by a single terminal initial.

The theory of independent histogens of the stem was introduced by SANIO (1864) and HANSTEIN (1868), and vigorously supported by these authors and by HABERLANDT (5). The researches of HANSTEIN (6) cover a wide field, in all forty-six genera including among the lower dicotyledons *Alnus*, *Populus*, *Platanus*, *Aesculus*, *Sambucus*, *Rhus*, and *Robinia*. He distinguished and illustrated in stem tips of these forms and others three histogenic layers giving rise to the epidermis, cortex, and vascular cylinder. He maintained that these distinct histogens appear at first divisions of the embryo, maintain their independence throughout the life of the plant, and

are increased each by its own group or series of initials. Other investigations on terminal growth in dicotyledons followed these of SANIO and HANSTEIN, some investigators questioning the constancy of occurrence and morphological value of these three layers, a few favoring the idea of a single terminal initial.

The conclusions of DOULIOT appeared, in the main, to support those of HANSTEIN, with less emphasis, however, on the idea of series of initials. He believed that in the great majority of dicotyledons the stem was terminated by three initial cells superposed for the epidermis, the cortex, and the central cylinder, and a small number of others by two initials only; the cortex and central cylinder in this case owing their origin to a single initial. The apetalous dicotyledons, according to DOULIOT, offered two conditions for consideration: (1) the case of two distinct initials, represented by the Urticaceae (*Humulus*), the Polygonaceae (*Polygonum*), the Cupuliferae, (*Carpinus*), and the Begoniaceae (*Begonia*); (2) the case of three initials represented by the Salicaceae (*Salix*, *Populus*).

Anatomical investigations since 1900, whether carried out from the point of view of phylogeny or from that of physiology, have offered slight contribution to our knowledge of the primary origin of tissues in the primitive angiosperms.

## Histology of axis

Since differentiation of the primary stem tissues both in *Quercus alba* and *Q. rubra* appears to be essentially the same, *Q. alba* has been selected for detailed description, and reference made to *Q. rubra* only at points of striking similarity or where marked structural differences exist between the two species.

The tip or promeristematic region of the seedling stem of *Q. alba* (epicotyl 2–5 cm.) occupies a zone approximately 0.05–0.06 mm. in length from the extreme tip to the point where it merges into the older meristematic tissues of the stem. This primordial portion is easily distinguished from the older meristematic tissues beneath by its small, uniform, isodiametric and densely protoplasmic cells. At the very apex of this growing point is seen a cell group, consisting of three to four cells which have the character and arrangement of initial or generative cells. In well differentiated material these

initial cells stand out distinctly at the summits of stems, both of *Q. alba* and *Q. rubra*, as four- or five-sided cells (lateral faces four to five in number), from which by tangential (anticlinal) divisions the dermatogen appears to have its origin. Figs. 14 and 18, transverse sections through the stem apex of *Q. alba* and *Q. rubra*, show an arrangement of the superficial rows of cells which points clearly to this apex group as the generative cells, at least of the epidermal layer.

Immediately beneath the initials of the epidermal layer may be seen another initial group, the cells of which (4 or 5 in number) occur in a more or less compactly cylindric or columnar formation. It is this subterminal initial group which in the writer's opinion gives rise to the periblem, in fact to the entire primary meristem, excepting the dermatogen. Periblem and plerome regions are distinguishable in this meristematic section of the stem, but their exact relation to their initial group can be clearly established only by a careful study of the embryonic plumule.

Distinct stem bundles obscure or indistinctly seen in transverse sections of stem tips of older seedlings may be distinguished without difficulty in longitudinal sections of the epicotyl at an early period of its development, especially in stages preceding leaf formation. As evident in fig. 16, a longitudinal section of the vegetative point of the stem axis of *Q. rubra*, the desmogen of the stem or cauline strands is differentiated early, and at a short distance from the lower initial group, apparently by repeated longitudinal divisions in the marginal cells of the plerome.

The epicotyl may reach a length of 1.10 mm. in *Q. rubra* (in *Q. alba*, 0.62–0.70) before the appearance of the first scalelike foliar appendages. After the development of the first four or five bud scales, so close is the succession of leaf primordia at the apex of the stem, and so reduced the extent and prominence of the apical meristematic area of the stem axis, that it becomes increasingly difficult to distinguish cauline strands from the foliar strands or to trace their origin. It becomes a serious question as to whether there are distinct stem or cauline bundles in this genus, for the procambium strands connecting the foliar appendages with the desmogen of the primary axis become the dominant strands of that axis.

A careful examination of serial transverse sections through stem

tips of the older seedlings (epicotyls 2.5–5 cm. in length) discloses no clearly defined desmogen to a point 0.06 mm. below the extreme apex. In this region, where the bases of the youngest leaf primordia merge into the stem tissues, there appear clearly outlined four small, isolated masses of procambial tissue. One of these marks the position of the central procambial or desmogen strand of the youngest leaf primordium. The other three are associated with the primordium of the second youngest leaf. So closely do the leaf primordia succeed one another at the apex of the stem, that their procambial strands appear almost simultaneously in the promeristem of the stem axis.

At the third node from the stem apex, or at a point 10 $\mu$ below that described in the preceding paragraph, there may be distinguished in the older meristem five distinct procambial masses, the largest of these being the downward extension of the central petiolar strand of the sixth leaf in order of development; the two stipular strands of this leaf describing partial arcs through the leaf base and cortex to the point where they unite with strands 1 and 3 in the stem.

A close study of nodal topography in the *Q. alba* discloses the fact that these five strands mark the position of the five outward projecting regions of the primary vascular cylinder, and hence indicate the region of entrance into the central cylinder of all leaf traces, both lateral and medium, of subsequently developed leaves. These strands may be followed through the stem a distance of two or three nodes before they merge with other bundles. Gradually the lateral leaf strands swing inward to take their position on the inward projecting points of the cylinder.

At lower levels in the stem the primary cylinder will be found to consist of a gradually increasing number of strands, the more prominent of which are directly traceable in origin to foliage leaves and bud scales enveloping the axis. These foliar strands, to be described in greater detail under leaf structure, have their origin at the bases of the leaf primordia, and in the course of their basipetal differentiation enter the region of the vascular axis, becoming the so-called "common bundles" of the primary cylinder.

No differentiation or development into mature vascular cells can be distinguished in the procambium of the stem tip of *Quercus* to a point 0.09 mm. below the apex of the axis. At this point ligni-

fication of elements is first seen at the innermost points of the older strands of that region. The order of maturation of the xylem elements of these strands is centrifugal.

## Leaf

The leaf of *Quercus alba* appears first as a small, conical emergence, at the apex of which is seen a group of two to three cells, the center one of which has the character of an initial cell. At a later stage (fig. 9) there appears in the epidermal layer of this primordium, at either side and several cells removed from the apical group, two slightly elevated cells which mark the point of origin of the two lateral lobes of the primordium. The leaf primordium thus becomes a three-lobed structure which extends around on either side of the stem apex, almost to the base of the preceding leaf. The central lobe of this primordium gives rise, through further development, to the petiole and blade of the leaf, the lateral lobes to the stipules (figs. 7 and 12, also tip of fig. 15).

For a time, or until the young leaf attains a size of from 0.22–0.25 mm., the stipular lobes grow rapidly, not only keeping pace with but exceeding the young blade, arching above that organ as a protection until the leaf apex passes from the embryonic into a permanent condition.

The differentiation of the desmogen or procambial strands takes place at an early period, and is first evident at the base of the leaf primordium. The elements of these strands may be distinguished from the surrounding tissues by the size and shape of the cells, indications of cellular activity and reaction to stains. This differentiation of procambial tissue occurs at three points in the leaf base. The first strand appears in a central position just beneath the central primordial lobe. Two lateral strands arise later, one beneath each of the stipular lobes of the primordium. The progression in development of these three strands is from this point both acropetal and basipetal. Acropetally they enter the three primordial lobes of the leaf, and their further development in this direction keeps pace with the growth of the blade and stipules, the central strand of the three being the middle nerve of the petiole and blade. Basipetally the differentiation of the desmogen strands progresses by repeated longi-

tudinal division of intervening elements of the leaf base and cortex, to the point where they connect with and become a part of the vascular axis. Their relation to and position in the primary cylinder have already been discussed under primary stem tissues.

While differentiation of these first procambial strands is in progress, and before the leaf reaches a size of 0.15 mm., vascular elements for the two lower lobes of the blade appear in the leaf base (fig. 7), one on either side of the central petiolar strand. In their progress through the leaf base toward the stem these lateral procambial strands of the blade meet and unite with desmogen of the stipules (fig. 2), both describing a short arc on either side, through the remaining section of leaf base and cortex, to the point of entrance into the primary cylinder.

With continued growth and expansion of the leaf, and in accord with the acropetal order of evolution of the leaf lobes, other desmogen strands arise from time to time, but in the base of the petiole. Those strands destined for certain of the intermediate lobes of the blade do not enter the vascular axis. In their basal differentiation, there occurs in the upper part of the leaf base an approximation and anastomosis of these lateral strands of the leaf with the stipular vascular elements described in the preceding paragraph. This is clearly illustrated in transverse sections in figs. 2, 3, and 4.

The vascular elements of the upper lobes of the leaf do not unite, either with the central petiolar strand or with the lateral blade and petiolar strands, but maintain a direct and independent course in their basipetal progression, entering the primary cylinder one on either side of the central petiolar strand. Thus the median leaf trace of *Quercus* (in the fully developed leaf) is seen to consist of three bundles, and the nodal structure of the typical leaf is described as trilacunar (leaf traces three to five in number with three gaps in the central cylinder, one median and two lateral).

The first lignification or thickening of the procambial elements appears in the cells of the leaf base, and progresses with the advance of these elements inward toward the stem and outward and upward toward the leaf tip. The first formed central strand of fig. 7 shows two, possibly three cells, apparently of the protoxylem, undergoing

thickening. There are no distinct phloem elements distinguishable until a later period (fig. 19).

## Bud scales

As previously noted, the first foliar appendages developed on the stem axis either of *Q. alba* or *Q. rubra* are not foliage but scale leaves (bud scales). These appear when the epicotyl reaches a height of 1.0–1.1 mm. Each young bud scale has four well defined desmogen strands which, like the procambial strands of the foliage leaves, have their origin at the bases of the appendages. These strands merge in pairs, and as two strands they approach the vascular axis.

The characteristic nodal structure at the point of insertion of the outer scalelike leaves or bud scales of *Q. alba* is shown in fig. 6, a transverse section through the basal portion of the plumule of one of the older seedlings. The bud scales illustrated have each at their base four vascular strands, each strand consisting chiefly of protoxylem elements. These strands unite in pairs in the base of the bud scale, forming two bundles, and in this condition they approach and enter the vascular axis both at the same point, thus causing but one gap in the primary cylinder. It is evident, therefore, that the first formed seedling nodes of *Quercus* are not of the trilacunar type usually associated with this genus.

Fig. 5, a transverse section through a portion of the same seedling as illustrated in fig. 6, but at a slightly higher level, shows the manner of connection of the vascular elements of the outer paired stipules with those of the central cylinder. Attention is called to the fact that each of these stipules has three strands which, like those of the leaf, have their origin in the bases of these stipular appendages. Near the point of connection with the stem the two stipules unite in a common base, their vascular strands meeting and uniting in pairs, thus forming three prominent bundles. These three bundles connect with the primary cylinder at two points, two of the three forming the median leaf trace, the third as a single lateral strand describing a partial arc through the leaf base to the lateral leaf gap.

## Discussion

Attention is directed in particular to the variable nodal anatomy exhibited in the seedling buds of the two species of *Quercus* examined. From the inner foliage leaves to the outer paired stipules and bud scales, there are evident three distinct types of nodal structure: (1) trilacunar (leaf traces three to five in number with three gaps in the central cylinder, one median and two lateral), characteristic of the foliage leaves; (2) bilacunar (leaf traces three in number with two leaf gaps, one median and one lateral), characteristic nodal condition at the point of connection of the outer paired stipules with the stem; and (3) unilacunar (two-strand vascular supply with but one gap in the vascular cylinder), found at point of insertion of the outer bud scales. In view of the facts here outlined, the question arises whether this simple unilacunar condition characteristic of the first formed leaves of the oak seedlings is to be regarded as a primitive character, or does it simply illustrate a case of reduction from the trilacunar type by the complete disappearance of the two lateral traces and gaps? Observations made in this investigation tend to support the former idea.

Facts brought forward thus far in the study of the origin of the vascular strands of the leaves indicate that the topography of the node, whether unilacunar, trilacunar, or multilacunar, is dependent upon or determined by the character of the organ developed at that node, rather than the reverse. Investigations based on the theory that the character of the node determines the nature of the nodal appendage (13) have failed to take into serious consideration the point of origin of the leaf strands, but appear to be guided by the vague but generally accepted theory that the leaf traces are put forth from the vascular cylinder, and that these developing traces exert a peculiar influence on the growing leaf primordia.

A recent text on plant anatomy (3) defines leaf traces as prolongations of the stelar vascular supply extending into the leaves, and states further:

> The term leaf trace is used in two somewhat different ways, as applied to any bundle which extends to a leaf, and to the complex of bundles which supply a given leaf. Since the trace is merely an extension of the vascular system of the

stem, either as a definite abruptly separated branch of that system, or as a strand gradually set off as a distinct part, there is not usually a definite point of origin of a leaf trace.

In the oak, the differentiation of the cells composing the leaf traces commences in the leaf base, and progresses from this point both outward toward the leaf tip and inward toward the central cylinder. The vascular strands, therefore, do not determine the character of the developing structures of the seedling but the primordia of the developing leaves or leaflike appendages start, and the vascular elements are differentiated in the tissues of these growing organs. Much the same idea has been suggested by COULTER and LAND (1) in their study of the dicotyledonous embryo of *Agapanthus umbellatus*.

## Summary

1. The primary stem of *Quercus alba* and *Q. rubra* shows two distinct initial groups, one for the dermatogen and a second (subterminal) common to both periblem and plerome. Distinct cauline strands may be distinguished in the primary tissues of the epicotyl only at an early stage of seedling development; such strands apparently taking their origin just beneath the initial regions and from the marginal cells of the plerome.

2. With the appearance of leaves or leaflike appendages at the stem tip, the vascular elements of these members (the foliar strands) become the dominant bundles of the primary cylinder. This fact no doubt has led to the commonly accepted idea that the primary cylinder of the more ancient dicotyledons consists only of bundles of the leaf trace.

3. The tissues of the leaf appear to originate from two initials: one for the epidermis, the second for the parenchyma and the bundles.

4. The procambial strands of the foliar organs originate in the bases of the leaf primordia. Differentiation of these strands progresses from the point of origin both basipetally and acropetally. The first thickening of xylem elements occurs in the procambial tissue in this region.

5. Both species of *Quercus* examined furnish evidence of variable nodal structure, the character of the node being largely determined by the nature of the developing foliar organs.

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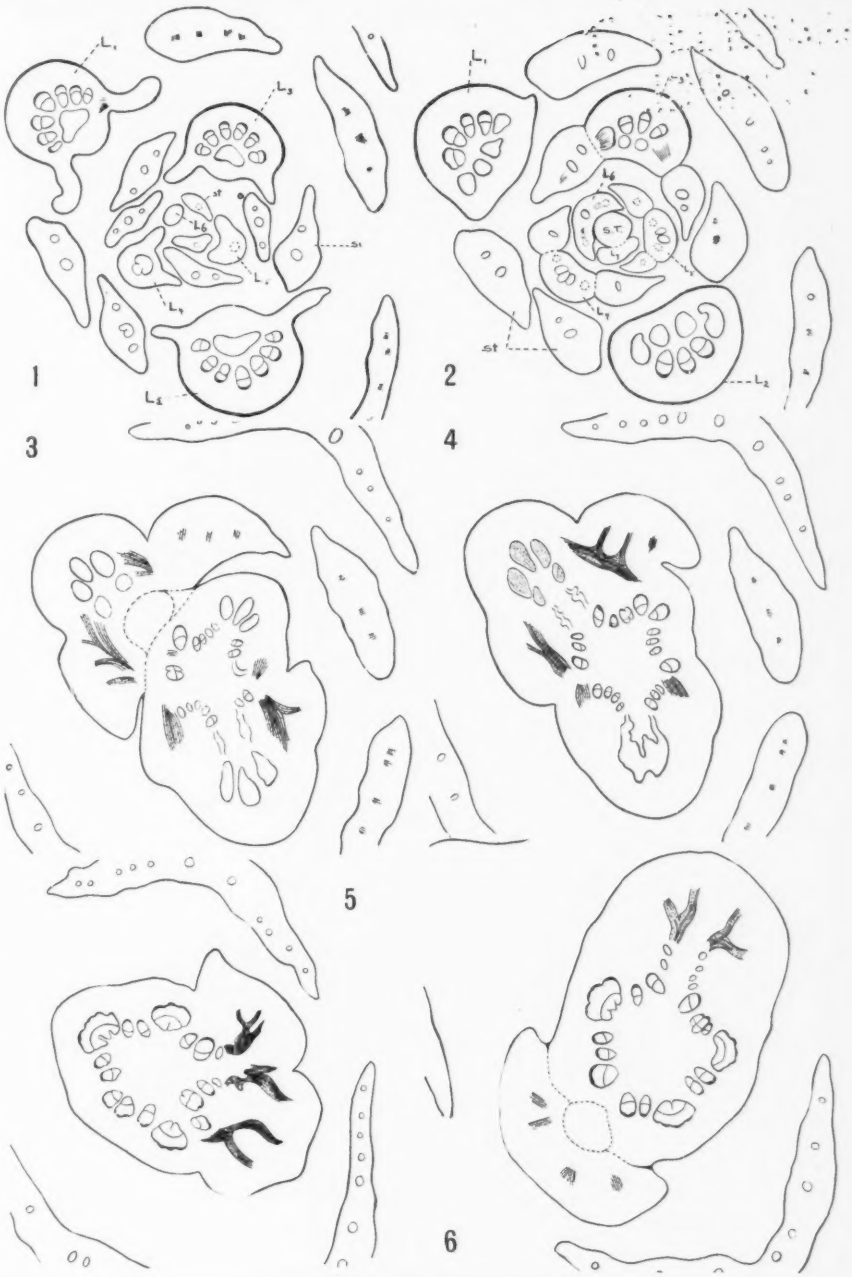


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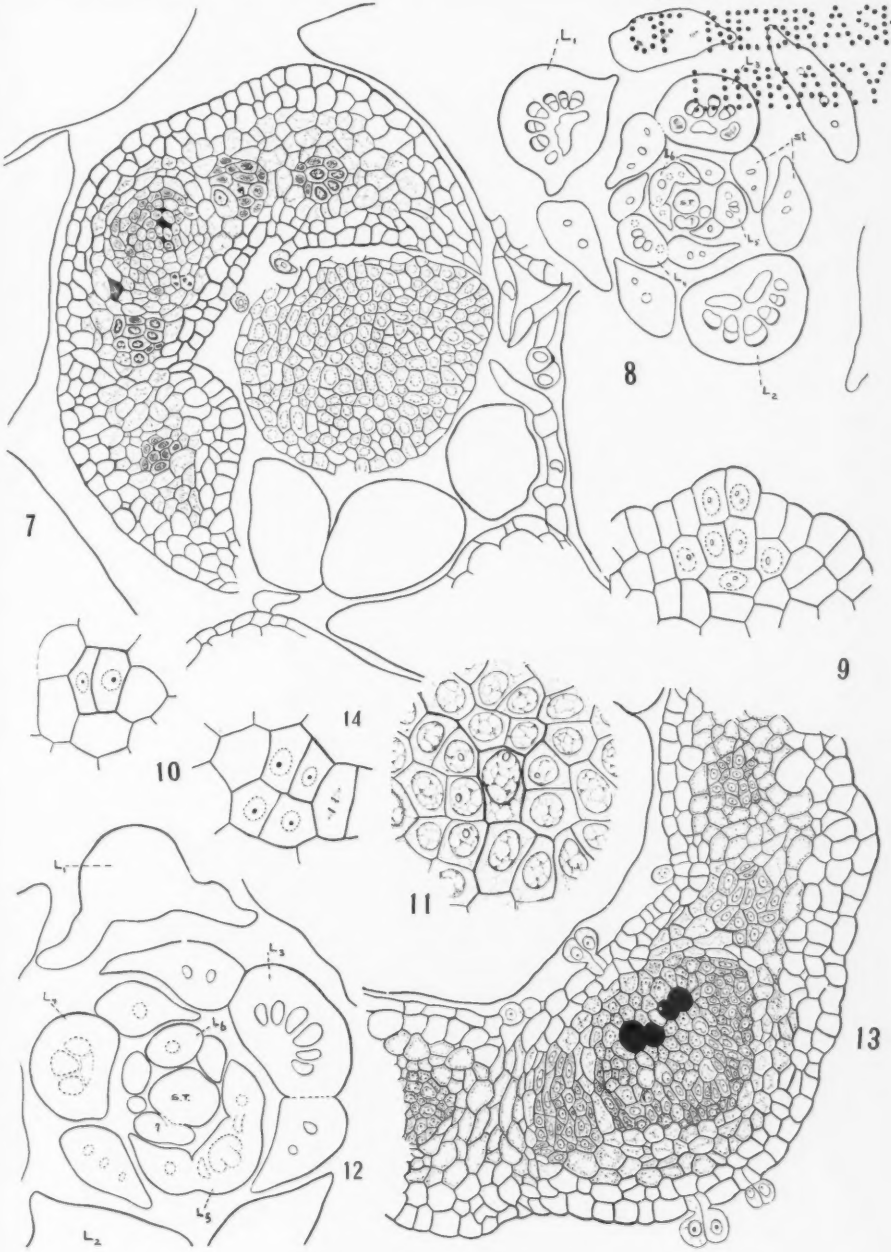


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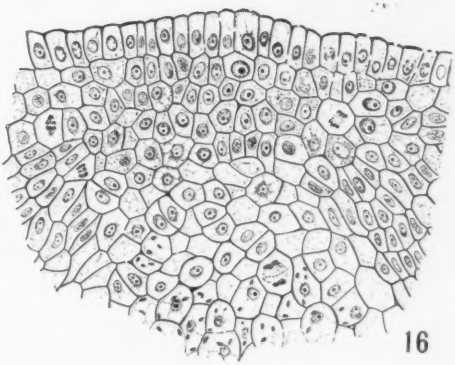

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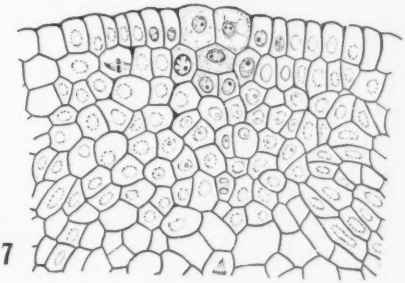

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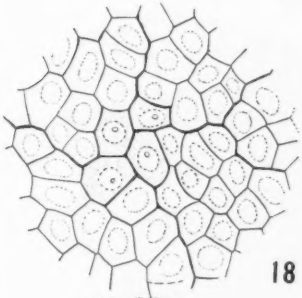

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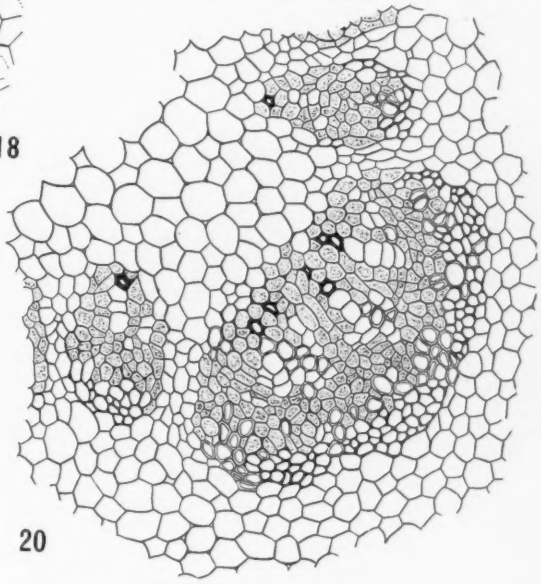

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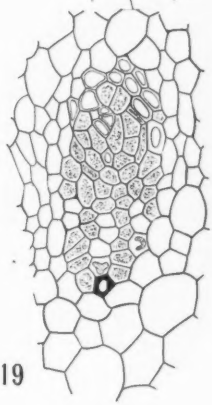

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LANGDON on QUERCUS

## EXPLANATION OF PLATES VII-IX

### *PLATE VII*

FIG. 1.—Transverse section through tip of epicotyl, showing arrangement of petioles and stipules of foliage leaves.

FIG. 2.—Section through tip of same seedling as fig. 1, at lower level; connection of stipules with base of petiole shown in younger leaves, also relation of stipular and petiolar vascular supply.

FIG. 3.—Manner of connection of vascular strands of foliage leaves with stem cylinder.

FIG. 4.—Same seedling, at 30 $\mu$ below point illustrated in fig. 3.

FIG. 5.—Transverse section illustrating manner of connection of vascular elements of outer paired stipules with those of central cylinder.

FIG. 6.—Characteristic nodal structure at point of insertion of outer scale-like leaves or bud scales; figs. 1–6, ×48.

### *PLATE VIII*

FIG. 7.—Detail of leaf no. 6, illustrated in outline in fig. 8; ×352.

FIG. 8.—Transverse section through tip of epicotyl at point where stem apex first appears: $L_1$, $L_2$, $L_3$, etc., foliage leaves numbered according to order of development; *ST*, stem tip; *st*, stipules; ×48.

FIG. 9.—Section through young leaf primordium; ×760.

FIG. 10.—Tip of stipule of embryonic leaf; ×912.

FIG. 11.—Tip of petiolar lobe of embryonic leaf, showing epidermal initial; ×912.

FIG. 12.—Transverse section of seedling tip; ×80.

FIG. 13.—Detail of fifth leaf, illustrated in outline in fig. 12; five procambial strands shown at base of petiole, three center strands merging, and one procambial strand at base of each stipule; ×352.

FIG. 14.—*Q. rubra:* stem apex showing epidermal initials; ×912.

### *PLATE IX*

FIG. 15.—*Q. alba:* longitudinal section of young epicotyl: *bs*, bud scales; *pr*, primordium of foliage leaf; ×48.

FIG. 16.—*Q. rubra:* longitudinal section of portion of stem apex; ×352.

FIG. 17.—*Q. rubra:* longitudinal section of portion of stem apex; ×352.

FIG. 18.—*Q. alba:* transverse section of stem apex showing epidermal initials; ×760.

FIG. 19.—Cross-section of young bundle; enlarged cells just beyond xylem elements cambium initials; ×456.

FIG. 20.—*Q. alba:* transverse section of stem of seedling near point of connection of scale leaves with stem; shows detail of primary cylinder at level in stem illustrated in fig. 6; ×352.

# A CORKY-BARKED MUTATION OF HEVEA BRASILIENSIS[1]

HARLEY HARRIS BARTLETT

(WITH SEVEN FIGURES)

This paper reports a new type of rubber tree in which true cork is produced from a cork cambium. *Hevea brasiliensis* mut. **granthami** (=**Hevea granthami**), mut. nov., differs from all other forms of the highly variable plantation rubber of the Far East in the production from a cork cambium of true cork, which appears in longitudinally arranged patches and ridges on young stems about one year old, and eventually attains a thickness of 16 mm. on the trunk (figs. 1, 2). Type, the original seedling, on Tanah Radja Estate of the United States Rubber Company, Asahan, East Coast of Sumatra; vegetatively propagated in Sumatra and Java. (Museum specimens, *Bartlett* 8747, H.A.P.M., Asahan, Sumatra, July, 1927, in Herb. Univ. Mich. & U.S. Nat. Herb.)

The largest area of plantation rubber under single management in the world is that of the Hollandsch-Amerikaansche Plantage Maatschapij (usually referred to in the East as H.A.P.M.) in Asahan, East Coast of Sumatra. H.A.P.M. is a subsidiary of the United States Rubber Company. Here had been planted, up to the year 1920, 5,000,000 trees. Since then over a million more have been set out. All of the trees have been continuously under scientifically supervised observation, since they have been utilized in a vast selection experiment, the object of which, of course, has been the acquisition of high yielding clones for budding, and of superior stocks upon which to bud them. In this selection work, without doubt the most extensive operation ever carried out for the improvement of a tree crop, a great many interesting variations of *Hevea* have come to light.

To the general botanist, who is not concerned with the economic problems involved, the most interesting tree among the 6,000,000 is

[1] Papers from the Department of Botany of the University of Michigan, no. 257.

the one which it is proposed to call *Hevea brasiliensis* mut. *granthami*, in honor of JAMES GRANTHAM, Director of the Plantation Research Department of the United States Rubber Company. In the

FIG. 1.—Type tree of *Hevea brasiliensis* mut. *granthami*, surrounded by ordinary smooth-barked trees; Tanah Radja Estate, Asahan, East Coast of Sumatra (Phot. H.H.B.).

preceding description *Hevea granthami* is suggested as an alternative name. If the origin of the new type were unknown, most botanists would consider it a distinct species. Those who give binomial names freely to every important type of woody plant will doubtless prefer the simpler nomenclature.

On account of the attention which has been directed to the single original tree of mut. *granthami* and its vegetative progeny, it may be stated with considerable certainty that there has been no other individual like it among the 6,000,000 trees on H.A.P.M. Further-

FIG. 2.—Trunk of type tree of mut. *granthami*, above tapping area (left), and corresponding picture of ordinary tree of same age and size (right); in mut. *granthami* the cork extends to the small branches, and is very conspicuous on trunk (Phot. H.H.B.).

more, since various other estates beside those of H.A.P.M. are under the control of the United States Rubber Company, a large additional number of trees is known to include none of the new type. It is therefore of the highest rarity. The writer interprets it as a seed mutation sufficiently diverse from the parent to rank as a distinct species.

Of course the status of the new form as a mutation rather than as a Mendelian segregate or recombination is subject to the usual criticisms, and at the present time is quite incapable of proof. Since parallel types occur in nature in other genera of woody plants, even the probability of a mutational origin is of no little interest from a general systematic and evolutionary standpoint.

FIG. 3

FIG. 4

FIGS. 3, 4.—Fig. 3, high budding of mut. *granthami* on ordinary smooth-barked stock (Phot. H.H.B.); fig. 4, low budding of mut. *granthami* on rough-barked but not corky seedling; roughness of stock due to fissuring of coarse thick bark (Phot. H.H.B.).

The best known cork-bearing tree, of course, is the Mediterranean cork oak. It would have been a bold mutationist indeed who would have ventured to hint at the derivation of such an apparently highly specialized type from a non-corky precursor by a single mutation, without being able to cite such a case as that of the sudden

appearance of *Hevea brasiliensis* mut. *granthami*. The writer ventures to predict that the mutational origin of corkiness in *Ulmus* might be observed without growing an excessive number of seedlings, since the character seems to have appeared many times in the evolution

FIG. 5

FIG. 6

FIGS. 5, 6.—Fig. 5, rough-barked ordinary seedling of *Hevea brasiliensis* which has been twice budded, once near base with a very smooth-barked type, and again on smooth scion with mut. *granthami;* the photograph demonstrates the hereditary distinctness of the three types; the stock has a dead, fissured outer bark but no cork; smooth-barked scion has only living bark, for there is a layer of green cells under the whitish epidermis; upper scion of mut. *granthami* has a cork cambium and abundant cork development (Phot. H.H.B.); fig. 6, low budding of mut. *granthami* grown without artificial support; tree has drooped over in a manner characteristic for the whole lot of over 130 buddings (Phot. H.H.B.).

of the species of this genus. Whether or not species of *Hevea* other than *H. brasiliensis* develop true cork the writer does not

know, and, writing from Sumatra, is not in a position to look into the matter.

The history of the *Hevea* rubber of the Malayan region is well known, and has recently been again reviewed by MAAS.[2] It is clear that all the trees of H.A.P.M. are descended from WICKHAM'S original introduction of 1876. The seedlings of the first generation were sent to Singapore from Kew. In 1883 and subsequently they bore seed, from which a second generation was grown. The pioneer estates of Malaya were initially stocked from the seeds of the second generation. The H.A.P.M. received most of its original stock from Cicely Estate near Teluk Anson, and Vallambrosa Estate between Kĕlang and Kuala Selangor. The later plantings at these estates were from seeds produced by their own trees, so the original H.A.P.M. stock belonged to the third and fourth generations from the WICKHAM introduction.

With regard to roughness of bark, there is a very considerable variation among rubber trees (figs. 3, 4). However, the common type of roughness is due to the fissuring of the dead outer layers of unusually thick bark, and does not extend far up the trunk. A very few seedlings develop cork on the main trunk, but not at all to the degree that characterizes mut. *granthami*, and not on the young growth. In mut. *granthami* the cork develops from a cork cambium just below the epidermis. It appears first in longitudinal patches with cross checkering. These patches become confluent and form irregular ridges by the gradual lateral differentiation of the cork cambium. The cork peels off very readily, disclosing the smooth surface of the cork cambium, which is scarlet on the main trunk of the original tree and varies to yellow on the smaller trunks of the vegetative progeny.

The original tree has had the lower part of the trunk repeatedly tapped. The renewed bark on the tapped area has developed a cork cambium near the surface, on which there is a sheet of cork 1 cm. thick. The cork on renewed bark has a smooth, irregularly checkered surface, since the cambium from which it grows is differentiated at once over the tapped area, and not in originally isolated longitudinal strips, as on virgin bark.

[2] MAAS, J. G. J. A., Het tapsysteem van *Hevea brasiliensis* op proefonderfindelijken grondslag. Arch. Rubbercult. **9**:1–221. 1925 (pp. 11–17).

The original tree of mut. *granthami* first came to notice because of its high yield of latex, which led to its being selected as a mother tree from which to make buddings. The numerous budded trees soon showed uniformly the cork ridges above the unions with the ordinary stocks (fig. 5). The genetic individuality of *Hevea* trees is only fully realized when large numbers of budded trees of the same age, strikingly identical, are compared with a block of seedlings. It then becomes obvious how large is the factor of heredity, and how

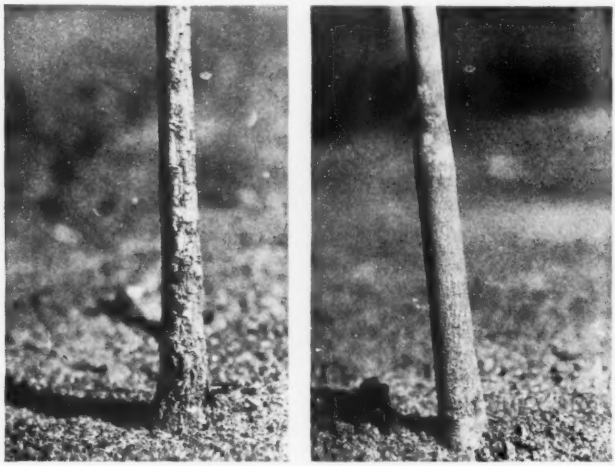

FIG. 7.—Young seedlings of mut. *granthami* (left) and ordinary *Hevea brasiliensis* of same size and age (right) (Phot. J. GRANTHAM).

relatively insignificant is the factor of environment in bringing about the diversity within an ordinary stand of seedlings. The buddings of mut. *granthami* proved its great distinctness from all other types, and led to an unsuccessful search of the plantations for other individuals.

Buddings of mut. *granthami* have the peculiarity that the trunk does not at first grow rapidly enough in diameter to support the heavy foliage. As a result all the trees bend over unless given artificial support (fig. 6). There is no reason to believe that this characteristic is necessarily associated with corky bark.

Approximately 200 seedlings have been grown from unguarded seeds of the original tree of mut. *granthami*. Three of them repeat the characteristic of the parent (fig. 7). Since most seeds of *Hevea* are the result of cross-pollination, it is a fair supposition that mut. *granthami* is a recessive. The three seedlings that have come true perhaps represent self-pollinations, and the remainder cross-pollinations. The three seedlings display thick cork on bark only a few months old.

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# A STUDY OF PREISSIA QUADRATA

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(WITH FIFTEEN FIGURES)

The adult gametophyte of *Preissia quadrata* almost rivals in complexity of structure that of its near relative, *Marchantia polymorpha*. Results obtained from a study of spore germination and gametophyte development in *Marchantia*[1] suggested a similar investigation in *Preissia*. HAUPT[2] says that a functioning apical cell does not occur in the embryo of the Marchantiales; however, he describes and figures a single cuneate apical cell for the adult thallus of *P. quadrata*, and also for *Reboulia hemisphaerica*.[3]

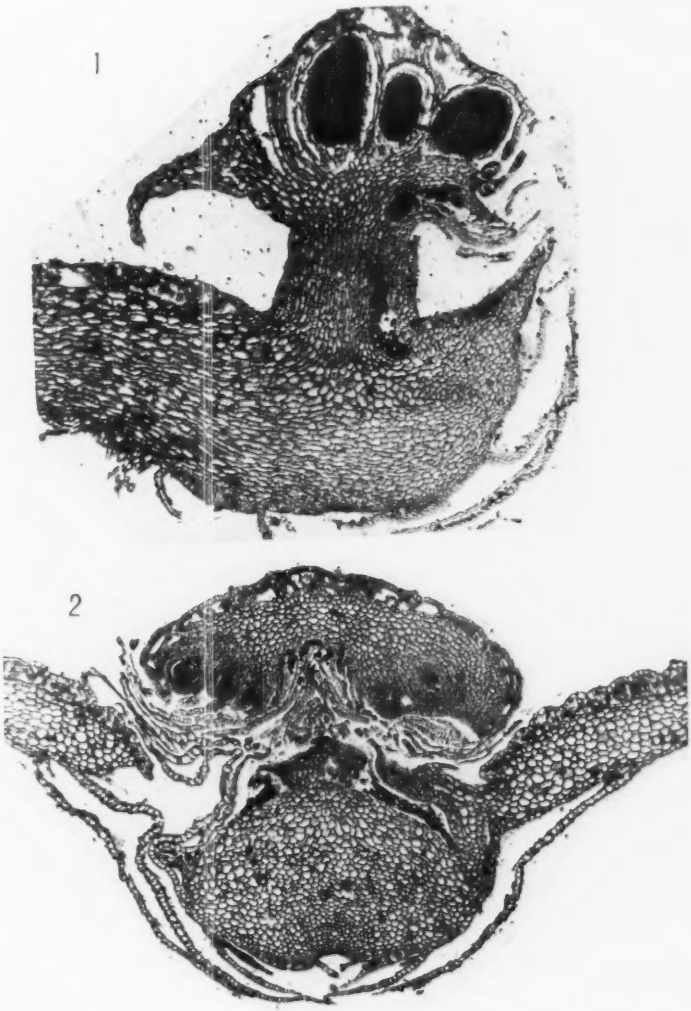
## Material

The material for this study was collected at Sinsinawa Mound, Grant County, Wisconsin, some in the autumns of 1924 and 1925, and more in the spring of 1926. The first consideration will be with the plants as they were found in this locality about October 10. As stated by HAUPT and some of his predecessors, *Preissia* is not only a monoecious plant, but there also occur mixed heads. A longitudinal section (fig. 1) of one of these plants shows the two-sided character of some of these heads. Of about ten heads that were apparently male, two proved to be mixed when sectioned. The other one of these showed a rather well developed sporophyte. It was at least as well developed as any of the embryonic sporophytes were at the close of the growing season. Sections of a typical male receptacle taken at right angles to the vertical axis of the stalk show that there are about thirty-six to forty antheridia in a single receptacle. A transverse section of a thallus bearing an archegonial head (fig. 2) shows the autumn condition of the young sporophytes. Although a group of three young sporophytes is seen at the left of the figure, there is a

[1] O'HANLON, SISTER MARY ELLEN, BOT. GAZ. **82**:215–222. 1926.

[2] HAUPT, A. W., BOT. GAZ. **82**:30–54. 1926.

[3] ———, BOT. GAZ. **71**:61–74. 1921.




FIGS. 1, 2.—Fig. 1, longitudinal section of tip of thallus through bisexual head; ×54; fig. 2, transverse section of thallus through archegonial head; ×66.

question whether it often occurs that more than two sporophytes in a single quadrant ever come to maturity.

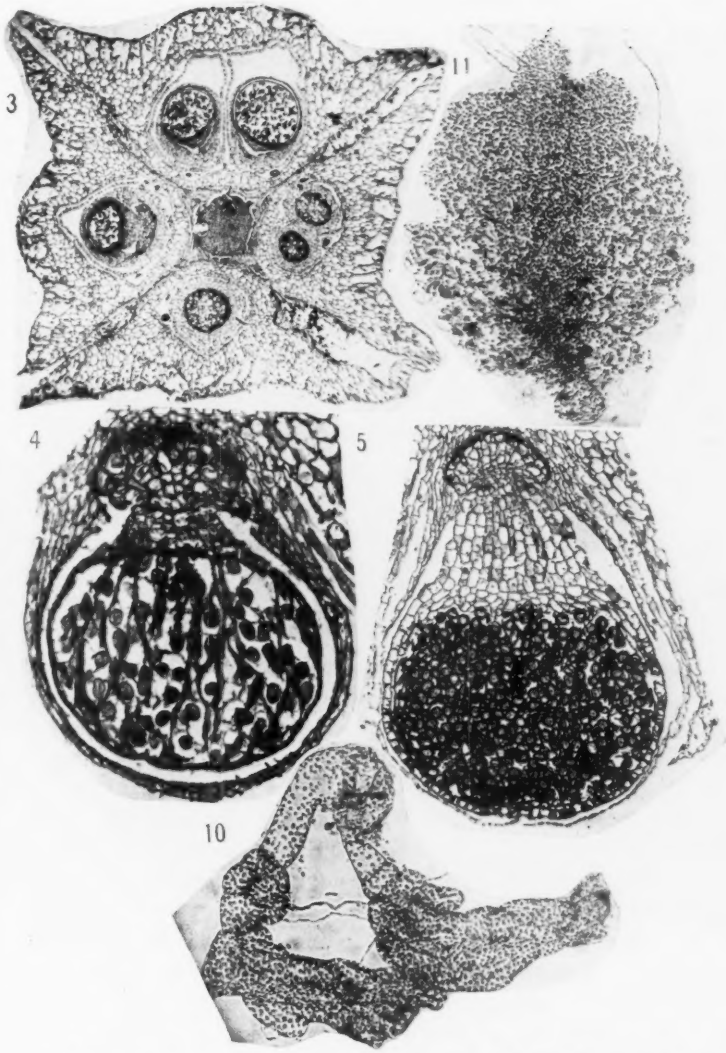
Plants collected May 10, and which reached the laboratory on the twelfth of the month, were more or less uniformly in the condition which is illustrated by a horizontal section through the archegonial receptacle (fig. 3). The number of archegonia in a quadrant ranges from three to six; the dominant number, the largest shown in this figure, is four. The average number of archegonia to a head probably does not exceed sixteen.[4]

The intracapsular tissue of the young sporophyte, found in most of the plants at this season, was differentiated into spore mother cells and elaters in an incipient stage of metamorphosis. Although the development of the sporophyte and the genesis of the spores were not sufficiently investigated to warrant a confident statement, it seems that the spore mother cells and the elaters of *Preissia* are of the same generation. This deduction is based largely on the comparative volume of the incipient elaters and that of the spore mother cells, as shown in fig. 6 *a*, as well as of sections, one of which (fig. 4) is a photomicrograph. At any rate, the ratio between the number of spore mother cells and the number of elaters is much less in *Preissia* than it is in *Marchantia* (figs. 5–6 *a-e*). Fig. 5 is a median longitudinal section of a mature sporophyte. In the laboratory, the period between the spore mother cell stage and that of the mature spore stage was about a week. Although fertilization probably occurs in every archegonium, the greatest number of mature sporophytes that were counted in any head was six, with not more than two to a quadrant.[5] In an examination of over one hundred heads, the range was from one to six, with an average of 2.98, and a dominant number of four sporophytes to a head. The average number of mature sporophytes in a head of *Marchantia polymorpha* was estimated at twenty-four.

The number of spores in a capsule of *Preissia* is estimated at 3000, with an average of nearly 9000 to a head. This is a marked re-

[4] The number of archegonia in a single group in *Marchantia polymorpha* is sometimes sixteen or over, with an average of eight groups to a receptacle.

[5] Many of the foregoing statements concerning *Preissia* are not new to the student of the Hepaticae and are merely repetitions of the facts stated by previous writers, including HAUPT, who has adequately cited and discussed the literature which is pertinent to this subject.




FIGS. 3–5, 10, 11.—Fig. 3, horizontal section through archegonial receptacle;×24; fig. 4, median longitudinal section of young sporophyte;×60; fig. 5, median longitudinal section of mature sporophyte;×65; fig. 10, twin thalli;×54; fig. 11, young gametophyte showing apical notch, mucilage hairs, and thickened midbody region;×178.

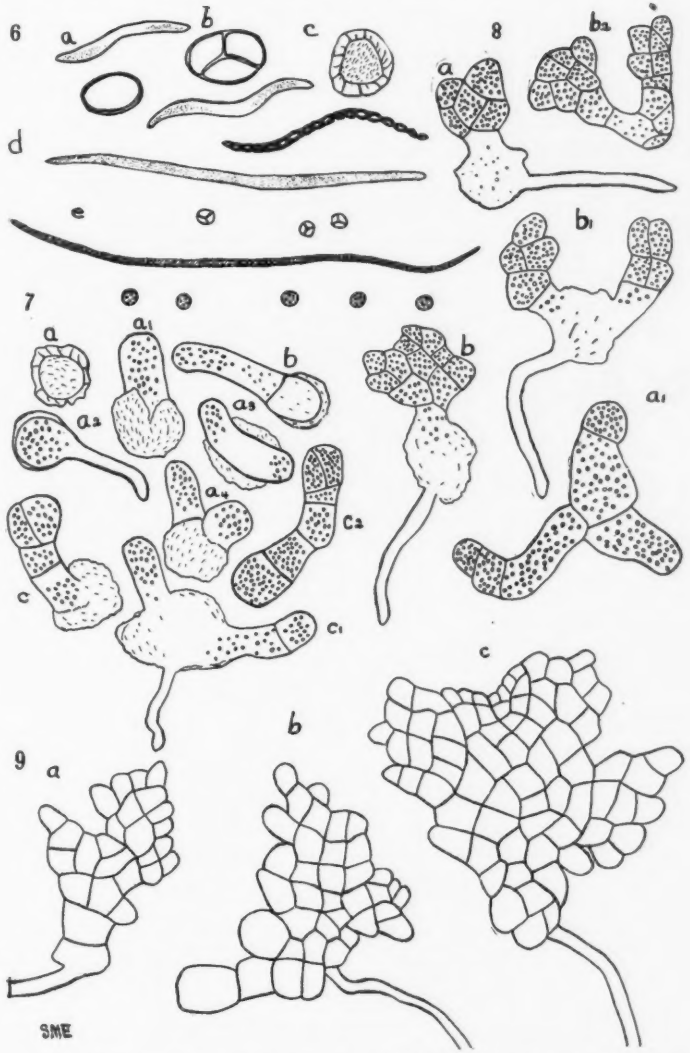
duction when comparison is made with *Marchantia*, in which the spore output for a single head is probably over 7,000,000. Notwithstanding this fact, however, when we consider the volume of the sporogenous tissue in the two genera, what seems to be such a striking advance in the case of *Preissia* is, after all, more apparent than real. It is true that the number of spores is greatly diminished in *Preissia*, and that the elaters are more numerous in proportion to the number of spores than in *Marchantia;* but a comparison of the size of the spores and the elaters of the two genera is disturbing to the theory that there is so much progress in the sporophyte of *Preissia* (fig. 6). The diameter of the ripe spore of *Preissia* is 75 μ. The diameter of the spore of *Marchantia polymorpha* is not over 18 μ. The elaters, although less numerous in proportion to the number of spores in a single capsule of *Marchantia*, still greatly outnumber the elaters in a sporophyte of *Preissia*, to say nothing of their greater volume. It is plain, therefore, that the real gain in the reduction of fertile tissue made by *Preissia* over its well known congener is in the paucity of the number of sporophytes, rather than in the actual reduction of the volume of fundamentally sporogenous tissue within the capsule itself.

## Spore germination

On May 19 some of the material which was collected May 10 was still in the spore mother cell stage, some was in the tetrad stage, while most of it was in the mature condition. On this date spores in all three stages of development were sown on porcelain plates kept moist with a mineral nutrient solution in glass chambers. These cultures were set up in an east window of a white walled room with north, south, and east exposures. The response made by the unripe spores was nil, but germination was evident in the ripe spores in about six days from the date they were sown, and it was 100 per cent. Tests were made on spores from the same collection between four and five months later, with results that showed persistent viability in about 10 per cent of the spores.[6]

Fig. 8 shows the variety of initial steps in spore germination. Probably there most frequently occurs the protrusion of a short germ tube as typified in *a;* often a rhizoid makes the first step as in $a_2$

[6] The spores of *Marchantia polymorpha* are 100 per cent viable for over a year.




FIGS. 6–9.—Fig. 6, spore mother cell and incipient elater, tetrad and more advanced elater, mature spore and elater, of *Preissia;* tetrad and ripe spore with corresponding stages of elater of *Marchantia polymorpha;*×132; fig. 7, mature spore and early stages in spore germination;×132; fig. 8, young gametophytes;×132; fig. 9, later stages in development of young gametophyte;×132.

and, less frequently perhaps, there appear simultaneously two cells which introduce a branching or twin condition ($a_3$–$a_4$). Sometimes there appears in the same culture a kind of filament not greatly unlike an algal form or moss protonema, as $c_2$. Experiments made with sowings on a liquid medium and in weak light gave even less satisfactory results than those which were obtained under similar conditions with *Marchantia* spores. It would seem that *Preissia* is even less inclined to a hydrophytic habit than *Marchantia* in these early stages, and of course is consistently more strictly mesophytic in its adult behavior.

One of the most interesting features in this study is the difference in the size of the cells in the sporelings of *Preissia* and *Marchantia*. The greater size of the cells in the sporeling of *Preissia* is accounted for by its much greater spore size. In the progress of the development of the young gametophyte, however, the size of the cells is gradually diminished so that in the adult thallus of *Preissia*, and, even long before that stage, the cells are no larger than those of *Marchantia*, perhaps, not even so large.

## Young gametophyte

Fig. 8 shows a series of stages in the development of the young gametophyte. The decrease in the size of the cells is due to the rapidity with which the successive mitoses occur. There is relatively little time for growth between each two mitotic divisions, and consequently there is rapid progress in the development of the young gametophyte. More advanced stages are seen in fig. 9. In *Preissia*, as in *Marchantia*, there always appears a distinct apex with its row of meristematic cells in at least one region of every progressive young thallus. When branching occurs, two or more such regions are established even very early (fig. 10). No more in *Preissia* than in *Marchantia* can we say that there is a single apical cell functional in the development of the young plant or plants which grow from a single spore that may be designated as *the* apical cell.

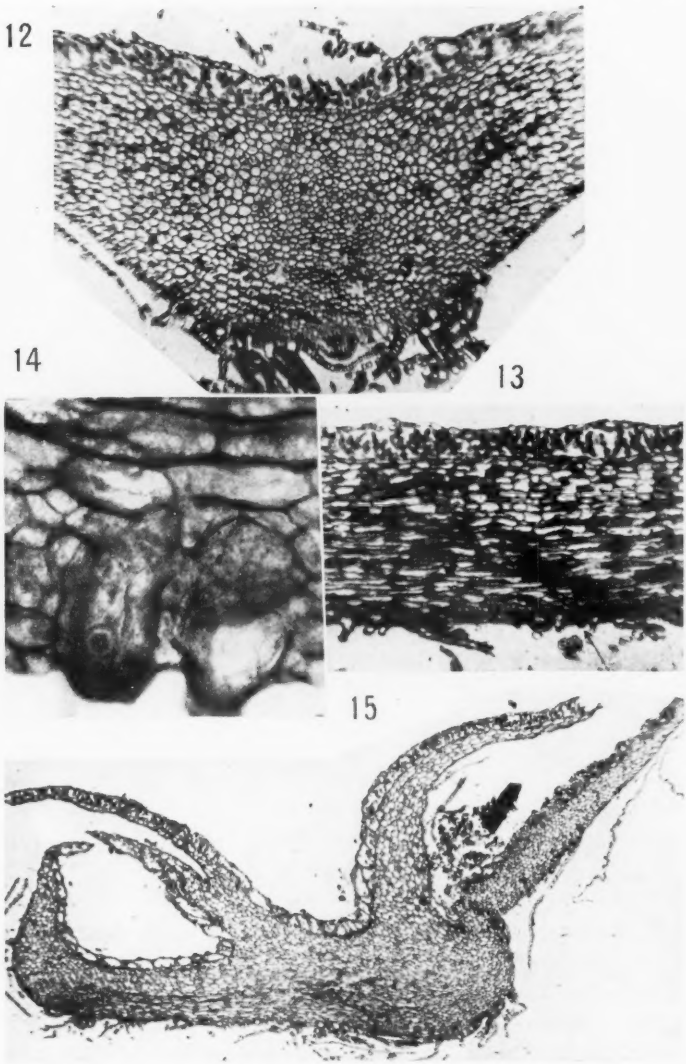
Since in *Preissia* there is no definite midrib in the adult thallus, cell division in the third plane of the young gametophyte is less restricted, making the thickened area more extensive than is the case in *Marchantia* at a corresponding stage of development (fig.

11). Contrary to the conditions in *Marchantia*, there are no special cells for the storage of essential oils in the young gametophyte of *Preissia*. The general contour of the young thallus also is more irregular than that of *Marchantia*. Anchorage is by mucilage hairs and rhizoids. The rhizoids of the young plants are of the plain walled type, as in *Marchantia*. Thus it is seen that the young gametophytes of these two genera are more or less similar in origin and structure, and seem to share certain resemblances with fern prothallia. There are some very obstinate and fundamental differences, however, even as there are in the adult plants.

### Adult thallus

A transverse section of the adult thallus (fig. 12), somewhat behind the apex, shows the thickness of the plant. There are thirty-five or more cells, exclusive of the chlorophyllose cells in the air chambers, in the thickest part of the thallus. A longitudinal section (fig. 13) of the thallus near the mid-body region shows the length of the sclerotic cells. These conducting cells are sometimes referred to as ventral cells. They are, if everything below the air chambers may be considered ventral; but the lowest cells of the thallus are least suggestive of tracheids, either in form or in function, as figs. 1 and 2 also indicate. A group of ventral cells (fig. 13) is highly magnified in fig. 14.

The potentialities of such cells as the one most prominent in fig. 14 are demonstrated by a regenerative plant. Fig. 15 is a more or less perfect longitudinal section through the anterior region of the thallus, from which there have grown three adventitious proliferations. Such vigorous cells as the one shown in fig. 14 must be the primordia of these innovations. Plants subjected to greenhouse conditions at the close of the growing season regenerated new shoots readily. Fruiting plants, that is, those bearing archegonial heads, failed to continue development. Possibly a quiescent period is necessary at the change of the season, but it seems more probable that the short daylight periods of the late autumn and early winter are insufficient for the maturation of the sporophytes. The relative senility of the cells in the receptacle would seem to account for their failure to resume development with the return of spring. Apparently their vital-




FIGS. 12–15.—Fig. 12, transverse section through midbody region of adult thallus; ×54; fig. 13, longitudinal section of thallus a little lateral to mid-body region; ×66; fig. 14, detail of fig. 13 showing ventral cells; ×535; fig. 15, section of anterior region of thallus showing three regenerative growths; ×33.

ity was sacrificed to the regenerative growths for which the shorter daylight periods are quite adequate.

## Summary

1. Twelve to sixteen archegonia are borne in each female receptacle, usually three to four in each quadrant, although as many as six were counted in a single quadrant of a receptacle.

2. Although fertilization is probably 100 per cent, the number of mature sporophytes in a single receptacle varies from one to six, the average number for over 100 heads was 2.98, the dominant number being four sporophytes to each head.

3. The sporogenous cells which metamorphose into elaters seem to be sister cells to the spore mother cells; therefore the number of spores is four times the number of elaters.

4. The number of spores to each capsule was estimated at about 3000; the average number for each head, therefore, would be nearly 9000.

5. The spores, although much less numerous than in *Marchantia*, are decidedly larger. Their diameter is about 75 $\mu$, while the diameter of the spore of *Marchantia polymorpha* is not over 18 $\mu$. The elaters of *Preissia* are smaller than those of *Marchantia*, although their number is greater in proportion to the number of spores.

6. The spores of *Preissia* germinate readily on a solid substrate, and they are viable for a shorter time than the spores of *Marchantia*, as only about 10 per cent of them germinated four or five months after their maturity.

7. The method of spore germination is similar to that in *Marchantia*, in that there is a variety of initial steps, with even greater scope for variation and individuality in *Preissia* than in *Marchantia*.

8. Branching is very common, and in some cases two thalli are initiated from a single spore cell. Early branching is frequent.

9. Unlike *Marchantia*, there are no cells for the storage of essential oils in the young thallus of *Preissia*.

10. The rhizoids of the young thallus, relatively few in number, are of the plain walled type as in *Marchantia*.

11. As there is no definite midrib in the adult thallus of *Preissia*, the thickening in the middle of the young plant is more extensive than is the case in *Marchantia*.

12. The general contour of the advancing young gametophyte of *Preissia* is often quite irregular, since there are so many actively growing points.

13. As in *Marchantia*, a distinct apex with its marginal row of meristematic cells is conspicuous in at least one region of the young thallus.

14. Finally, as in *Marchantia*, there is no single cell functional in the development of the young gametophyte of *Preissia* that may be designated as *the* apical cell.

The writer is indebted to ROBERT G. GUTHRIE for the preparation of the negatives used in the illustrations, and to Sister AUDREY KERBER for collecting some of the plants.

ROSARY COLLEGE
RIVER FOREST, ILL.

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# CURRENT LITERATURE

## BOOK REVIEWS

### Evolution and classification of cacti

A most interesting little volume has recently been published by BERGER,[1] who has long been a leading authority, not only on the growing but also on the classification of succulents, especially of the cacti. He has been a pioneer in developing our present classification of this difficult group. For many years, as Curator of the Thomas Hanbury Garden at La Mortola, Italy, he grew many of these plants, and had exceptional opportunities to study many species which are rarely found in European gardens.

As is well known to all students of this group, its classification has been very difficult to present in a logical way. This has probably been due to the reluctance of botanists to recognize enough genera. For instance, in his *Species Plantarum*, published in 1753, LINNAEUS reduced all the cacti, some 15 genera, known in his time to the single genus *Cactus*. PHILIP MILLER, botanist as well as gardener, who knew many of these plants living restored the genera *Opuntia*, *Cereus*, and other striking ones, but which those who followed LINNAEUS were slow to accept. Afterward from time to time new genera were described, but these too were reduced by succeeding botanists to synonymy. Then, in 1900, KARL SCHUMANN published his great monograph of the family, but he recognized only 21 genera. A few years afterward OTTO KUNTZE condensed the family into the three genera, *Cactus*, *Pereskia*, and *Pterocactus*, the latter two containing but 14 species, thus leaving almost the entire family (1000 species or more) in the genus *Cactus*, as proposed by LINNAEUS 150 years before!

About 1910 BERGER published one of the most suggestive little papers on the classification of cacti which had yet appeared, and which formed the basis of the classification developed in the monograph of the family published by the Carnegie Institution in 1921–23. BERGER had brought together at La Mortola a large number of cacti, where they had grown luxuriantly, and many had flowered and fruited under his eye. With information obtained from the living plants themselves he prepared this new classification of the genus *Cereus*.

On the origin of the cactus family BERGER has not been able to throw any new light. He agrees with DE CANDOLLE and KARL SCHUMANN that the nearer relationship is with the Aizoaceae. This relationship, however, is most remote. This fact, along with the great diversity in the cactus family itself, seems to suggest a very ancient origin. As the family is wholly American, one would

[1] BERGER, ALWIN, Die Entwicklungslinien der Kakteen. 8vo. pp. iv+105. Jena: Fischer. 1926.

expect to find a closer relationship with some American family than with an Old World one. It is not unlikely that the intergrading family or families do not now exist. Unfortunately geology does not throw any light upon this interesting problem, for no cactus fossil of any kind has ever been found. This is certainly very remarkable, for if the family is so very old, as we are now inclined to believe, some records must have been made in the rocks. Although the cactus plants are made up mostly of water, the spines and hard seeds of many of them might easily be preserved. It has been suggested that the reason these are not found is because the cacti grow in the deserts away from the swamps and lakes. But in many places, such as Lower California and the Islands of the Gulf of California, great cactus plants are found just on the water's edge, which on dying must fall into the sea, while all the streams which flow through these deserts must carry great quantities of cactus débris to the sea.

As to the development in the family itself, BERGER thinks it originated from some *Pereskia*-like ancestor which had normal branches and leaves, and which had a tendency to become succulent, and perhaps without spines. These grew in the tropics on the border of forests. From these main stems were developed two lateral branches, each with a definite type of seed. From one was developed the genus *Cereus* and its relatives (Cereeae), and from the other *Opuntia* and its relatives (Opuntieae).

The classification follows closely that of BRITTON and ROSE. For instance, BERGER divides the family into three tribes, Pereskieae, Opuntieae, and Cereeae. The last and largest is exactly that of BRITTON and ROSE, while in the other two he transfers the genus *Mahuenia* from the second tribe to the first. The genera are the same except that he raises two subgenera of *Opuntia* to generic rank, namely, *Brasilopuntia* and *Consolia*. He also has described as new the genera *Stephanocereus* and *Roseocactus;* he recognizes 129 genera in all. His arrangement of the genera is entirely new and deserves careful study. I have no hesitation in saying that this little book is one of the most important contributions to the study of cacti which has yet appeared.—J. N. ROSE.

## NOTES FOR STUDENTS

**Taxonomic notes.**—EVANS and MEYROWITZ[2] have published a list of the lichens of Connecticut. It is stated that the list includes "records from 79 towns" in the state, and contains 231 species and 65 genera. An interesting contrast is made with the lichen flora of certain other New England states, in the following statement: "Over 700 forms are known from Maine, 375 from Vermont, and nearly 400 from Massachusetts." This contrast probably accounts for the statement that "the study of Connecticut lichens is still in its early stages."

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[2] EVANS, A. W., and MEYROWITZ, ROSE, Catalogue of the lichens of Connecticut. Conn. State Geol. and Nat. Hist. Survey. Bull. 37. pp. 49. 1926.

HUNT[3] has published a list of the Uredinales of New England. The number of species listed is 204, distributed in families as follows: Coleosporiaceae 7, Uredinaceae 34, Aecidiaceae 163. The genera are described, and under each is a list of species with their hosts. Much the largest genus is *Puccinia* with 98 species, and next to it is *Uromyces* with 35 species. Nearly 700 species of host plants are listed, the genera with the largest representation being *Crataegus* and *Carex*.

LEONARD[4] has published a revision of the North American species of *Scutellaria*. This genus is generally distributed in temperate and tropical America. It seems that no full presentation of the group has appeared since its publication by BENTHAM in DE CANDOLLE'S *Prodromus* in 1848. The older names and the specific characters represented a very tangled maze. LEONARD has recognized 62 species, no new species having been found in the United States, but 7 new species from the tropical region of North America are described.—J. M. C.

**Essential elements for plants.**—The term "the ten essential elements" has attained almost a state of sanctity in plant physiological circles. As SOMMER and LIPMAN[5] point out in their recent paper, the list of ten elements assumed to be the only ones needed for the growth of green plants was, with the exception of the later substitution of iron for silicon, the same as that given by DE SAUSSURE in 1804. Thus for more than a century this concept was held, although ash analyses showed a large number of other elements present in plants. With the improvement in technique in rather recent work, the idea became quite general that, while the ten elements were the only ones necessary in the sense that there could be no growth without them, the presence of other elements improves the growth of plants. These added elements were called by some "stimulants." Still more recently MAZÉ, WARINGTON, BRENCHLEY, MCHARGUE, and others have performed experiments which indicate very strongly that we must add to the list of ten a number of other elements, these being not merely stimulants but absolutely indispensable for plant growth. This literature is reviewed by the authors.

SOMMER and LIPMAN worked with zinc and boron, and instead of showing the need of these elements for one plant, as was true of some of the work of others, they showed that they are needed by several plants of widely separated families, which indicates that they are needed by all green plants. All possible precautions were observed to exclude impurities. Specially purified salts were

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[3] HUNT, W. R., The Uredinales or rusts of Connecticut and the other New England States. Conn. State Geol. and Nat. Hist. Survey. Bull. 36. pp. 198. 1926.

[4] LEONARD, E. C., The North American species of *Scutellaria*. Contrib. U.S. Nat. Herb. **22**:703–748. 1927.

[5] SOMMER, A. L., and LIPMAN, C. B., Evidence on the indispensable nature of zinc and boron for higher green plants. Plant Physiol. **1**:231–249. *figs. 13*. 1926.

used. The plants were grown in a small greenhouse constructed in a larger greenhouse. By screening the ventilators and other means a practically dust-free atmosphere was obtained. Redistilled water was used in making up the culture solutions, and the plants were grown in glass containers made of a kind of glass giving only an insignificant amount of the element being studied to the culture solution. If it was possible to do so, the seed was cut from the seedling soon after germination.

The results are presented in the form of photographs. The contrast between the plants grown with zinc and boron present and those grown without one or the other of these is very striking, and certainly gives strong evidence that these elements are essential for the growth of green plants, and do not serve merely as "stimulants." Considerable other work has been done by the authors on aluminum, silicon, and chlorine, and the results of this will be presented in later papers.

BRENCHLEY and WARINGTON[6] have published a recent paper showing that boron is essential for various plants, including several legumes and the melon. Various cereals and candytuft completed their development in the absence of this element. The question is raised whether there is a class distinction here, or whether the latter plants merely require so little boron that there is enough in the seeds to supply their needs. The latter interpretation would seem to be the correct one, for SOMMER and LIPMAN'S work strongly indicates the need of boron by barley. As to the physiological significance of boron, BRENCHLEY and WARINGTON state that in the case of the broad bean their work suggests a connection with the absorption or utilization of calcium. They also performed experiments to determine whether the nature of the substratum on which the plants were grown, the condition of aeration about the roots, the hydrogen-ion concentration, and other features affected the need of certain plants for boron.

Thus it would seem that the term "the ten essential elements" is now obsolete, at least when used in its original sense. The concept, however, still retains the significance that the ten are the elements needed in the largest amounts. But that other elements are indispensable for the growth of plants certainly seems proved by the evidence, and it would seem justifiable to add at the present time zinc, boron, and manganese to the list. Probably other elements will have to be added later, as in fact certain work already indicates.—S. V. EATON.

**Investigation of "glacial relics."**—TURESSON[7] has made an interesting analysis of the well known *Poa alpina*, by growing side by side plants from various localities of Sweden and Norway, and observing their differences in

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[6] BRENCHLEY, WINIFRED E., and WARINGTON, KATHERINE, The rôle of boron in the growth of plants. Ann. Botany **41**:167–187. 1927.

[7] TURESSON, GÖTE, Contributions to the genecology of glacial relics. Hereditas **9**:81–101. 1927.

structure and in earliness. He finds that the species is composed (in Scandinavia) of three ecotypes: (1) *alpinus*, a dwarf alpine type with high water requirements, early blooming; (2) *subalpinus*, tall with moderate water requirement, widely distributed, especially in the alpine region; (3) *pediacus*, tall, glaucous, with low water requirement, late blooming, restricted to the lowland in isolated localities.

*Poa alpina* found in lowland situations has usually been considered a relic of the first flora which appeared after the melting of inland ice, but TURESSON thinks that the first plants to follow the retreating glaciers must have been early blooming and resistant to cold. He holds that the present lowland form could not have been evolved from alpine populations by selection of biotypes fitted for lowland conditions, because no such biotypes could exist in the rigorous climate of the time. It is concluded, therefore, that the lowland forms are from other stock and came in during a later and warmer period. *Poa alpina*, like many other species, was subjected in the Ice Age to a great destruction of its low altitude biotypes, and hence has been able to occupy only small and isolated areas in the lowlands. No such depauperization of alpine biotypes took place, so the species is now well represented at high altitudes.

Students of plant geography in this country could probably find answers to some of their problems by determining the ecotypes of their species with TURESSON'S method of growing together specimens from different localities and altitudes. It is possible that in America also the "relic hypothesis" has been overworked.—F. RAMALEY.

**Influence of light on seed germination.**—ELISABETH KOMMERELL[8] has published the results of her investigations on the influence of light of various wave lengths on the germination of seeds. She conducted quantitative experiments, using the seeds of *Lythrum salicaria* and *Nicotiana tabacum*. The seeds were illuminated in a thermostatic chamber by light of various wave lengths obtained from an Osram lamp. The energy of the different portions of the spectrum was made approximately equal by inserting screens consisting of photographic plates blackened to various degrees. The measurements of energy of the incident light were made with a bismuth silver thermopile and a Paschen galvanometer. The time of exposure of the seeds was adjusted to bring out differences in different regions of the spectrum, since with too long exposure these differences were not apparent.

The results indicate that the percentage of germination varied directly with the wave length, and the author concludes that the germination of seeds is a photochemical process following the EINSTEIN Photochemical Equivalence law. This law may be expressed as $N=\frac{Q}{h\nu}$. $N$ is the number of molecules in-

[8] KOMMERELL, ELISABETH, Quantitative Versuche über den Einfluss des Lichtes verschiedener Wellenlängen auf die Keimung von Samen. Jahrb. Wiss. Bot. **66**: 461–512. 1927.

volved in the primary photochemical reaction; $Q$ is the energy absorbed from the radiation and used in activating $N$ molecules; while $h\nu$ is the value of the quantum of frequency $\nu$, and is directly proportional to the frequency. It is apparent that with a constant amount of energy absorbed, there will be more molecules transformed in the region of long wave lengths and low frequencies, since there the value of the quantum $h\nu$ is smaller. A complete test of the law requires the determination of $N$, $Q$, and $\nu$.

In the case of the germination of seeds the number of molecules involved is unknown, but if (1) the percentage of germination may be taken as a measure of the number of molecules reacting, and (2) the energy absorbed may be considered as equal in all portions of the spectrum when the incident radiation is made equal, then more germination would be expected in the longer wave lengths, and there would be a linear relation between wave length and percentage of germination. However, if the preceding assumptions (1 or 2) do not hold, then the finding of a linear relation would lose the significance attached to it.

Many attempts have been made by photochemists to confirm the EINSTEIN law, and the results to date are not very encouraging, due to the great experimental difficulties and the uncertainty regarding primary and secondary processes, even in relatively simple chemical reactions. Under these circumstances it seems almost hopeless to seek a confirmation of the law in the complex totality of reactions represented by the germination of a seed.—F. WILCOXON.

**Intersexualism in Arisaema.**—MAEKAWA[9] has discovered in *Arisaema japonica* the occasional appearance of intersexual spadices. The arrangement of flowers on such a spadix is very distinct, the staminate and pistillate flowers not intermingling, but appearing in distinct groups. All of the intersexual spadices in succeeding years were transformed into pistillate spadices. It was noted that the intersexual specimens are rather frequent in plants that were wounded in former years.—J. M. C.

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[9] MAEKAWA, T., On intersexualism in *Arisaema japonica*. Japanese Jour. Bot. 3: 205–216. 1927.

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